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WITH THIRTY-EIGHT PLATES, AND NUMEROUS
FIGURES IN THE TEXT



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A SYNECOLOGICAL STUDY OF USAMBARA, TANGANYIKA TERRITORY, WITH PARTICULAR REFERENCE TO BIRDS

By R. E. MOREAU, M.B.O.U., C.M.Z.S.
(East African Agricultural Research Station.)

(With Plates I and II and two Figures and two maps in the Text.)

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INTRODUCTORY NOTE.

ELSEWHERE (Moreau, 1934) I have discussed, with reference to the peculiar ecological conditions found generally in mountain forest areas of Tropical Africa, the criteria that a descriptive study of this nature must take into account.

In order to keep the scope of this paper within manageable bounds I shall concentrate on describing conditions found in the mountains, which form islands of luxuriant vegetation in the great South-east African steppe. Reference to the lowlands will be made only to the extent necessary to provide a setting for the mountains and a standard of comparison for montane conditions.

The local data have been accumulated during four years' residence in the Usambaras. Identification of the birds dealt with rests upon the collection described by Selater and Moreau (1932 and 1933), where the authors of the names used are quoted. To avoid constant repetition in the pages that follow, the bird names will be given here without their authors. A bibliography of Usambara ornithology is given by Selater and Moreau (1932, pp. 496, 497), but

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the works there mentioned are practically all systematic and can contribute nothing to an ecological study.

I have received help from many sources. That given by Mr P. J. Greenway, Botanist at this Research Station, has been invaluable. He has supplied or brought up to date all the many botanical names used in the pages that follow, and he has made numerous identifications of botanical material for me. Special acknowledgment must also be made to my wife, who has been a constant collaborator in the field, and to Mr L. Wigg of the Tanganyika Forests Department, who has furnished data of forest composition and rainfall.

TOPOGRAPHY AND SOIL.

Topography.

The Usambara Mountains form part of the ancient crystalline complex of East Africa. They consist essentially of huge blocks of gneiss upthrust within a diamond-shaped area of about 2000 square miles between $4^{\circ} 24'$ and $5^{\circ} 16'$ S. and $38^{\circ} 10'$ and $38^{\circ} 48'$ E. (see Map 1). From the western edge of the Usambaras Kilimanjaro is visible 120 miles to the north-west; from the eastern, a wide prospect of the Indian Ocean, only 25 miles away, with Pemba Island on the horizon.

The Usambara group itself is divided into three sections by trench-like valleys which have evidently been determined by tectonic action and deepened by erosion. The diagrammatic section (Fig. 1, printed on p. 6) is taken along a line drawn approximately south-east and north-west from the mouth of the Pangani River through Amani and Lushoto. West again of the Mkomasi Valley the Pare Mountains rise, forming a connecting link with Kilimanjaro. It will be seen that the Lwengera Valley makes a complete break between the East and the West Usambaras. Nevertheless, the indications are that it has not been an important factor in the distribution of the mountain flora and fauna. The Middle Sigi (or "Zigi", see maps) Valley, which cuts off the Mlinga-Magrotto ridge, the easternmost and comparatively small outlier of the mountains, is almost as well-marked a feature as the Lwengera Valley.

All these major features and many of the minor ridges on the plateaux have a common direction, north and south. Gigantic faulting in two directions accompanied the upthrust of the mountains. The result is that they are bounded on every side by scarps. On the southern edge of the West Usambaras sheer cliffs reach in one place the great height of half a mile. The plateaux themselves are deeply graven, a feature that cannot be conveyed in such a diagram as that offered here. The ridges of the East Usambaras are with one exception of uniform maximum height, between 3000 and 4000 ft. The slopes, are, however, everywhere steep, and the practicable routes very limited in number. At the northern end of the East Usambaras the outlying mass of Hindu rises to 4900 ft. It is of great interest that in the restricted area—about 3 square miles—so provided above 4000 ft. several species of birds abound that are

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characteristic of a similar altitude in the West Usambaras, but unknown elsewhere in the East.

At this point it may be well to recall that although the Usambara plateaux present, when viewed from the surrounding country, such strikingly mountainous features, the altitude of the highest ridges of the East Usambaras hardly exceeds that of the peneplain of south and east Central Africa. The basin of Victoria Nyanza is actually at a greater height above the sea than Amani.

All the features of the West Usambaras are on a bigger scale than those of the East. Looking across the gulf of the Lwengera Valley the prospect is of a grand confusion of ridges piled one behind the other, to culminate in the Shume and Shagai "Divide," at over 7000 ft. Even in the middle of the plateau this ancient eroded landscape presents headlands and cliffs 500 ft. high. Minor outcrops of rock appear frequently.

Naturally in such a country there is very little standing water. Almost everywhere the rivers are wild mountain torrents dashing among boulders and through gorges, often overarched by forest trees. Such conditions do not favour an extensive population of water birds; but on the other hand these streams possess the interest of maintaining their mountain characteristics to a much lower altitude than anywhere else in East Africa. The Lwengera River is a torrent until at only 1100 ft. above the sea it emerges abruptly into the valley that bears its name. Past Amani the Sigi River falls nearly 1000 ft. in 5 miles, and only becomes a river of deep slow reaches haunted by cormorants and crocodiles when it has arrived within 600 ft. of sea-level.

Soil.

The soils of the Usambara Mountains are predominantly light brown or reddish, often intense in colour. They do not vary greatly in mechanical composition. In spite of their high nominal clay content, from 25 to 55 per cent., the soils are usually "loams" or even "sandy loams," much more rarely "clay loams" or "clays" in texture, if texture is judged by permeability to excess water, friability in the hand, etc. The fact is that the constitution of the local clay fraction is fundamentally different from that of temperate European clay. The top-soil is usually somewhat shallow with a content of organic matter higher than would be expected from its colour. It is resistant to erosion. The potassium content of these soils is probably, and the calcium content almost certainly, low.

In bottom-lands in the foothills and at the base of the scarps the predominant soil is nearly black in colour, with the properties of a well-lubricated sand in a clay matrix but with no higher actual clay content than the reddish soils. Under the name of Black Cotton Soil it is well known and dreaded by travellers in the rainy seasons¹.

¹ I am indebted to **Mr G. Milne**, Soil Chemist at the East African Agricultural Research Station, for the information on which the foregoing two paragraphs are based.

Areas that are obviously sandy do not occur in Usambara, and nowhere are there exposures of sand such as bank-dwelling birds prefer in Europe. But the channels made by the roots of the forest trees are preserved indefinitely in the soil and are used as ready-made nesting-holes.

ALTITUDINAL ZONATION.

Some authors have divided the life zones of Equatorial Africa into Tropical, up to about 5000 ft. (or the isotherm of 20° C.), succeeded by Subtropical to 10,000 ft., and thereafter the Temperate and Alpine Zones (cf. Bowen, 1932). On the other hand Shantz and Marbut (1923) avoid the term Subtropical, using Tropical and Temperate.

Neither of these systems of division can be satisfactorily applied to the Usambara Mountains. Evidence will be produced to show that on biotic grounds the mountains, with a maximum height of 7500 ft., are divisible into three zones. For example, the transition from the East African Lowland to the East African Montane (Avifaunal) Subregion is in great part accomplished between 1500 and 3000 ft. in the small space of 2 miles on the scarp below Amani. The extent of this critical zone is too small to be appreciated from maps of ordinary scale, and Map 2 has been drawn up mainly with the object of depicting it.

I shall call these zones Lowland, with its upper limit at about 2500 ft., Intermediate from 2500 to 4500 ft., and Highland. I have avoided giving them names with direct temperature connotations for two reasons. It would have been difficult to avoid terms of that nature that do not conflict at some point with the general nomenclatures referred to above; and, whatever conclusions may ultimately seem justifiable, it is desirable at this stage not to adopt terms implying the prime and direct importance of temperature.

The limits of the Lowland, Intermediate and Highland Zones are indicated approximately in Fig. 1. It will of course be understood that in nature there are no hard and fast lines. Owing to the topography the distribution of land surface within the three zones is peculiar. A total of about 900 square miles rises above Lowland limits, about 750 in the West Usambaras, 140 in the East, and 5 on the Mlinga ridge. But, while 98 per cent. of the plateaux east of the Lwengera fall within the Intermediate Zone, only about 200 square miles of the West Usambara plateau fails to reach the Highland Zone. Of this 200 in the Intermediate Zone three-quarters are accounted for by the north-east and south-east corners of the plateau. Most of the remainder represents a narrow belt of rocky slope halfway up the encircling scarp. In other words, the Intermediate Zone practically exists only to the extent of 140 square miles on the East Usambara plateau and 150 square miles on the eastern edge of the West; while the Highland Zone, with an area of about 550 square miles, appears only on the west plateau and the top of Hundu.

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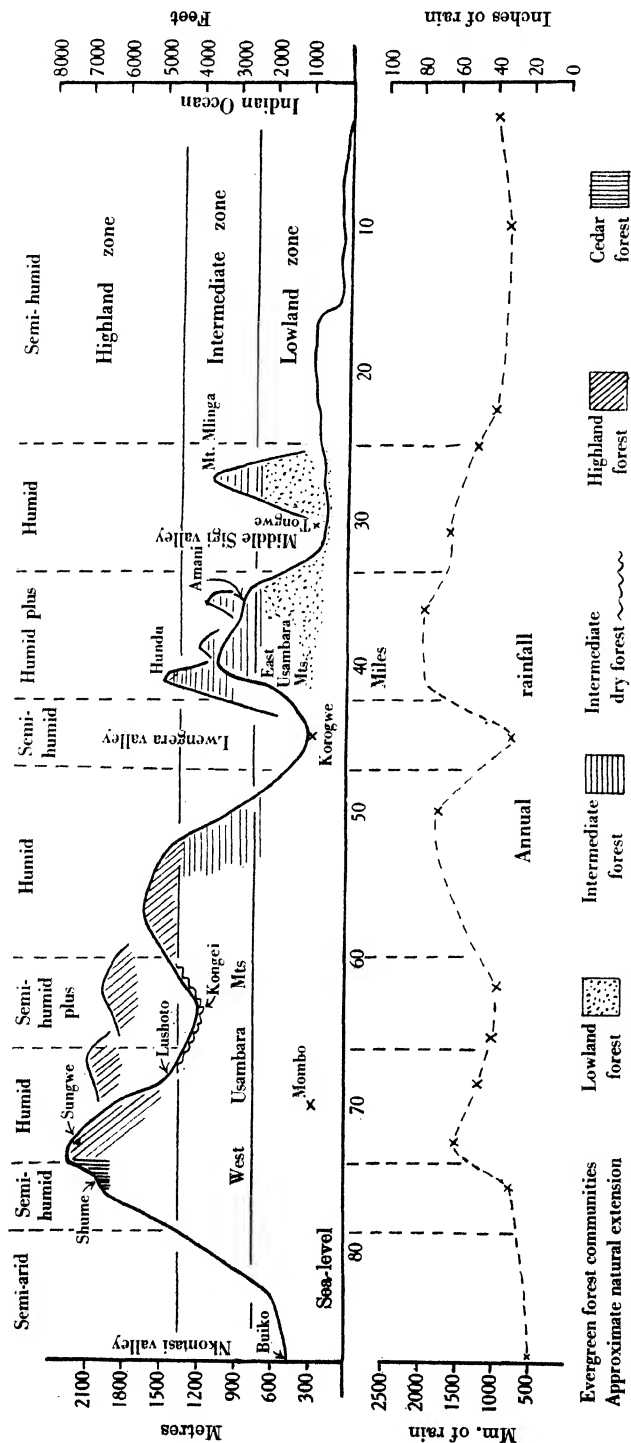


FIG. 1. Diagrammatic section of the Usambara Mountains, south-east—north-west.

THE STANDARD CLIMATE.

The data in this section are derived from the records of ordinary meteorological stations. As has been pointed out (Moreau, 1934), most bird habitats engender a distinct eco-climate, and consequently the climate inhabited by most birds is not the "general" or standard one¹. In describing the bird habitats an indication will, where possible, be given of the direction in which the eco-climate of each differs from the standard, and it is only by applying the appropriate modification factor to a standard climate that the true range of temperature, etc., of any species can ultimately be obtained.

Most of the data quoted here and used in Figs. 1 and 2 are derived from the *Meteorologische Beobachtungen* in successive volumes of the *Mitteilungen aus den Deutschen Schützgebieten*, especially Schlikker (1915) for rainfall, and from information supplied to me by the British East Africa Meteorological Service. Owing to the importance of the Usambara Mountains in German colonial policy the network of recording stations has been unusually close for a tropical area.

Rainfall.

Throughout Usambara nearly half the year's rain comes in the "Long Rains" of March, April and May, and a good deal of the remainder about November. This is in conformity with the precipitation along the neighbouring coast. On the East Usambara Mountains, in the Middle Sigi Valley, and on the eastern edge of the West Usambara plateau although the rainfall shows the same two peak periods it is exceptionally well-distributed. For example at Amani there are on the average only 3 months in the year with less than 4 in. of rain and no two of those are consecutive.

The south-east—north-west line chosen for the section in Fig. 1 is considered to be typical of mountain conditions with the exception noted later. It will be seen that the rainfall drops a little below 40 in. as the coast is left behind. It rises sharply as the foothills of the East Usambaras are approached, and reaches nearly 80 in. on the plateau². The Lwengera Valley lies in a rain-shadow, with less than 40 in. at its southern end (Korogwe) and probably under 30 at its northern. But figures of over 70 in. are reached again by a very rapid transition on the eastern scarp of the West Usambaras. Towards the centre of that plateau the rainfall drops again below 40 in., recovers to nearly 60 as the "Divide" is reached, and falls sharply to under 30 on the extreme western edge.

¹ In the paper quoted I used the term "general" to indicate the climate recorded at a meteorological station by standard methods of exposure. "Standard Climate" is perhaps a better description and to that phrase I shall adhere.

² Pre-war records for Sigital (1800 ft., immediately below Amani) average about 60 in. Records for the last three years from Tongwe Mission, at 800 ft. in the bed of the Sigi Valley, indicate an average there of nearer 70 in.

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The records available for a number of other stations in the mountains show that this rainfall curve approximately holds good for other south-east—north-west sections except on the eastern edge of the West Usambara plateau. There a sudden reduction takes place from south to north in consequence of a transverse ridge. Three stations on the south of the line of section figured, i.e. in the south-east corner of the West Usambaras, record rainfall between 80 and 95 in.: two stations within 10 miles to the north show 50. An intermediate figure of 70 in. has been taken for the western lip of the Lwengera in the diagram.

For the foot of the mountains we have only a few records, all on the south side. Allowing for the fact that there is evidently a rapid diminution of rainfall within a short distance of the actual foot of the scarp, there appears to be a falling off from south-east to north-west, from about 50 in. under the East Usambaras to less than 40 at Korogwe, 35 at Mombo and 20 in the Mkomasi Valley.

Temperature.

Fig. 2 gives the annual means, the mean maxima of the three hottest months and the mean minima of the three coldest for all stations where they

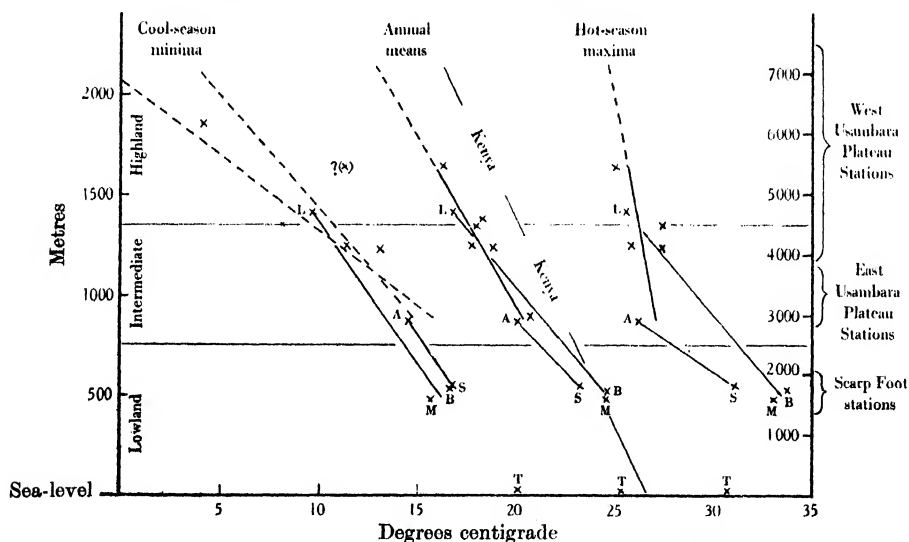


FIG. 2. Temperature-altitude gradients in the Usambara Mountains.
For explanations see text (p. 9).

are available for at least 3 years¹. The data are such as to warrant an attempt to sketch temperature-altitude gradients for the Usambara Mountains as a whole.

¹ All three figures are not available for every station. For some we have only annual means; for another, where recording broke down in the hot season, only the minima. The sea-level records (Tanga) are not taken into account in this discussion because they come from the shore-line, within the full influence of the sea breezes.

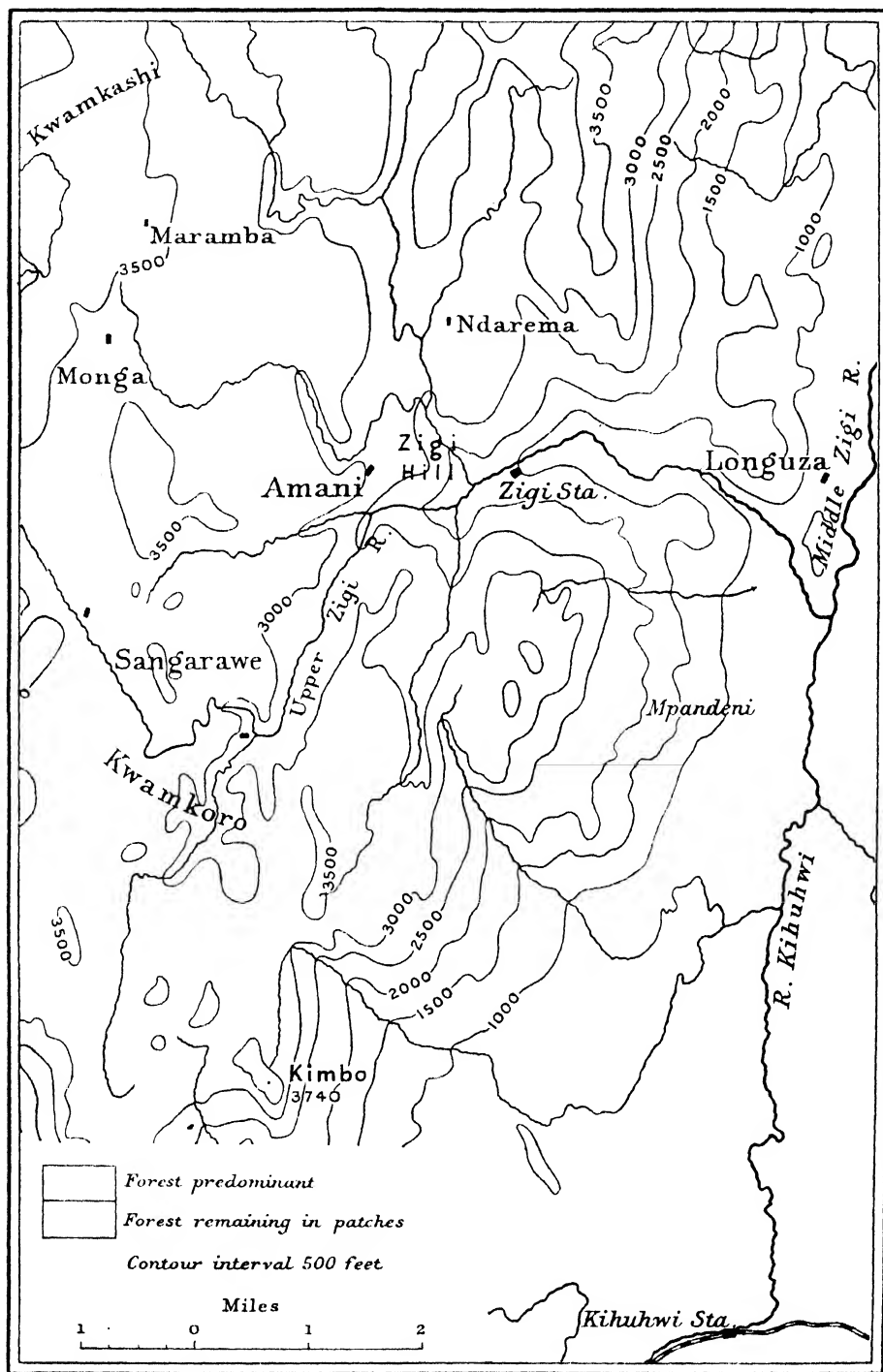
For stations on the plateaux, i.e. those from 2800 ft. upwards, the records of maxima and of annual means clearly lie close to straight lines, so close that we are justified in drawing these two temperature-altitude gradients for elevations rising above the plateaux¹. But if these gradients are produced downwards, i.e. to altitudes on, and at the foot of, the bounding scarps, it is obvious in the maxima, and appreciable in the annual means, that the Lowland figures do not lie on the same gradients as those from the plateaux, although, as may be seen from Fig. 2, they do accord with the general Kenya gradient. The Usambara Mountain temperatures are exceptionally low for their altitude and latitude and in particular lower than those for Kenya at corresponding altitudes (see Moreau, 1934, Fig. 1). It is now evident that this difference is attributable to the scarps, as might have been expected on theoretical grounds, and that the temperature gradients on the scarps must be different from those for elevations on the plateaux. We can gain some idea of what these scarp gradients actually are (*a*) for the East Usambaras by joining points *A* and *S*, representing Amani and the Sigi Valley; and (*b*) for the West Usambaras by joining *L* (Lushoto) and the points midway between *M* (Mombo) and *B* (Buiko). This leads to the interesting result that the hot-season maxima fall off much more rapidly with altitude, but the cool-season minima if anything more slowly, on the scarps than for elevations on the plateaux. Thus on the Amani-Sigi scarp (see Map 2), the lower station of which is rather shut in, the difference in maxima is actually 5° C. per 1000 ft., compared with 1° C. per 1000 ft. for plateau elevations. The West Usambara scarp gradient is a little under 3° C. per 1000 ft. in maxima. Naturally, with the small number of stations available exact figures cannot be insisted on, but the general trend is clear. Moreover, these gradients for unshaded situations are paralleled by the gradients between figures obtained under the Evergreen Forest canopy at 3000 and 1150 ft.

Thus it is clear that on the scarps the most rapidly changing element of the temperature is the hot-season maxima: on the plateaux it is the cool-season minima. The difference is one that requires to be borne in mind for future discussion.

It may be noted that the annual isotherm at the upper limit of the Lowland Zone does not quite coincide with that commonly accepted for the upper limit of Tropical conditions, which is 20° C. (Chapin, 1923 and Bowen, 1932). That isotherm falls within the Intermediate Zone in Usambara, at 3000 ft., while in Kenya it occurs at nearly 5000 ft., which in Usambara is in the Highland Zone.

Frosts are unknown below at least 5000 ft. I am informed by residents on the West Usambara plateau that at about that height ground frosts have been known to occur. These would doubtless not be associated with a temperature

¹ The minima are more scattered. This may be due in part to the fact that night temperatures are extremely sensitive to small details of siting. The point marked ?(x) is wide of the general grouping and is doubtfully correct. Two minima gradients have therefore been indicated, respectively including and ignoring this point. The truth probably lies between the two of them.



MAP 2. The Amani area: East Usambara.

so low as 0° C. in the screen. At 6000 ft. frosts measurable in the screen are not rare. At Shume temperatures down to -3.1° C. have been recorded.

The range of temperature at a number of local stations is given in Table I. "Forest" denotes that the neighbourhood is predominantly forested; "(Forest)," that the area is one of mixed forest and clearing; "Open," that forest has disappeared in the vicinity. The figures bear out the generalisation that the daily range, and to some extent the absolute annual range, tends to increase with the altitude and with the openness of the country.

Table I.

Station	Altitude in ft.	Nature of country	Daily range		Absolute Max.	Absolute Min.	Extreme range	No. of years	Average annual range
			Mean	Max.					
1. Tanga	60	Sea shore	6.7	10.7	35.1	16.9	18.2	4	15.6
2. Mombo	1593	Open	12.6	19.1	39.8	13.6	26.2	3	23.8
3. Sigi Valley	1794	Forest	8.9	15.8	34.8	11.2	23.6	4	21.0
4. Amani	2843	Forest	8.5	14.0	32.3	9.5	22.8	6	19.9
5. Ambangulu	4000	Forest	—	—	32.0	7.0	25.0	4	—
6. Bumuli	4060	(Forest)	9.7	18.3	31.2	8.1	23.1	2	22.8
7. Lwandai	4417	Open	14.4	23.2	30.5	2.3	28.2	3	27.3
8. Lushoto	4580	(Forest)	—	—	30.5	2.8*	27.7	4	—

* Questionable. It is recorded in one of the three hottest months of the year.

TYPES OF CLIMATE.

As pointed out elsewhere (1934) absolute precipitation as measured in a rain-gauge is, by itself, no measure of the biological potentialities. Apart from distribution, which is probably nowhere in our area so bad as to be decisive biologically, temperature is of prime importance in determining whether a given number of inches of rain shall produce a dry climate or a humid one.

In the absence of atmometric data a very rough but serviceable idea of the kind of climate resulting from the interaction of rainfall and temperature in various parts of the Usambaras may be obtained by plotting the annual rainfall and the mean annual temperatures (derived from Fig. 2) against McDougall's curves (1925). Table II gives the details for a number of important points on the section taken for Fig. 1. Where the resultant falls definitely in the wetter half of a division the positive sign has been added, in the drier the negative. It may be noted in passing that in this classification the term "Arid" is reserved for fully desert conditions.

Table II.

Locality	Altitude in ft.	Mean temp. ° C.	Annual rainfall in.	Type of climate
1. Coast	—	25	40	Semi-humid
2. Middle Sigi Valley	600	24	65	Humid Minus
3. Amani	3000	20	77	Humid Plus
4. Lwengera Valley	1000	24	(30)	Semi-humid Minus
5. Eastern edge of West Usambaras	4500	17	70	Humid Plus
6. Middle of West Usambaras	4000	18	35	Semi-humid
7. Lushoto	4500	17	47	Humid Minus
8. Sungwe	7000	(13)	57	Humid
9. Shume	6400	15	30	Semi-humid

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It should be added that on the plateaux, especially where large areas of forest remain, the rainfall is supplemented by so-called "occult precipitation." At Amani, for example, heavy dews form on nearly every night in the year, and wet white fogs frequently envelop the ridges and permeate the forests, especially above the Lowland Zone.

In testing the extent to which this classification is suited to the local conditions we have to rely mainly on vegetation as an indicator. It can certainly be said that by this criterion its adoption is justified. For one station a numerical check can be applied. The mean annual humidity at Amani as calculated from the readings at 8.30 a.m. and 1.30 p.m. has been recorded as 84.4 per cent. (*First Ann. Rep. East Afr. Agric. Res. Sta.* p. 3). This accords satisfactorily with the above classification of the climate as Humid Plus.

Rainfall data are available for twenty-five stations on Map 1. Utilising the mean annual altitude-temperature gradients arrived at in Fig. 2 the extension of the three main types of climate, Semi-arid, Semi-humid, Humid, over most of the area can be calculated. The results are projected on Map 1. Only for the northern lowlands are no measurements in existence, and there the limits of the climatic types are sketched on the basis of the vegetation.

VEGETATION.

TYPES OF VEGETATION.

The vegetation of Usambara has been described in some detail by Engler (1903 and 1910) who had personal experience of the country¹. His studies are not on modern lines such as it would have been desirable to draw upon for our present purpose, but still it is generally possible to adopt his divisions for the purpose of describing the bird habitats that are conditioned by vegetation. I have endeavoured to use the nomenclature of Shantz and Marbut (1923), Tansley and Chipp (1926), and Phillips (1929 and 1931), but their generalised studies often do not provide terms applicable to the peculiar Usambara conditions.

On this basis the vegetational divisions used are those given below. The brief synonymy with each will reduce the necessity for long lists of plant names in describing habitats. Prominence can thus more readily be given to plants ascertained to be of importance in avian economy. It need hardly be said that the study of specific food relations is in its infancy, and that nothing in the nature of a catalogue of edible fruits can be attempted. So much indeed remains to be learnt of the botany—and the entomology—of the area, that even the best-preserved stomach contents must often go unidentified.

¹ **Eichinger** (1914) has dealt particularly with the distribution of the Grasses. Kliem's *Die Vegetationsformationen Deutsch-Ost-Afrikas* (Langensalza, 1907) is a compilation with little to recommend it.

(1) *Closed Evergreen Forest Formation.*

(a) Lowland E.F. Community = "Untere Regenwald" and "Uebergang" of Engler (1910, pp. 292 and 289 respectively).

(b) Intermediate E.F. Community = "Regenwald" and "Tropische Regenwald" of Engler (1910, p. 296)¹.

(c) Intermediate Dry E.F. Community = "Obere trockene oder wasserarme Regenwald" of Engler (1910, p. 324).

(d) Highland E.F. Community = "Hohenwälder" of Engler (1910, pp. 332 and 336); "Subtropical Evergreen Forest" of Phillips (1929, p. 363; 1931, p. 370); "Temperate Rain-Forest" of Shantz and Marbut (1922, p. 32).

(e) "Cedar" Forest Community (Phillips, 1931, p. 370) = "*Juniperus*" of Engler (1910, p. 335).

(f) Highland Evergreen Scrub Community = "Gebirgsbusch" or "Gebirgsbaum-Steppe" of Engler (1910, p. 327); "Subtropical Evergreen Scrub" of Phillips (1929, p. 358).

N.B. Forests (a) and (b) might be regarded as subdivisions of the "Tropical Rain Forests", and (d) and (e) of the "Mountain Forests," of Tansley and Chipp (pp. 207-9), but the specific and even generic composition is different.

(2) *Deciduous Parkland Formation.*

This is of great importance and extent in Tropical Africa generally. In one form or another it entirely surrounds the Usambara Mountains, but, as stated in the Introduction, it is not the intention in this study to differentiate the subdivisions of Parkland or to describe their birds in detail. For the present purpose, then, only two general terms will be used:

(a) Savannah, covering the "Open Woodland" and "Orchard Country" of Tansley and Chipp (p. 205), the "Dry Forest" (= "Miombo") and the "High Grass—Low Tree Savana" of Shantz and Marbut (pp. 37, 50); the "Grasreiche Baumsteppe" and "Trockenwald" of Engler (p. 262); the "Mischwald" described by Engler as occurring on the sides of the Middle Sigi Valley (p. 293); and the "Combretum—Other spp.—Open Woodland" of Phillips (1931, p. 366).

(b) Thorn Country of Tansley and Chipp (p. 206), covering the "Acacia—Desert grass Savana" of Shantz and Marbut (p. 63) and the "Dornbuschsteppe" and "Grasarme Dornbaumsteppe" of Engler (pp. 255-60).

¹ This and the Lowland Forest cannot be made to fit into Phillips' 1931 classification. His "Lower Level Tropical Evergreen Forest" has a list of species very different from that of the Usambara Lowland Forest. His description of the forest association next in altitude, viz. the "Upper Tropical Evergreen Forest," suffers from over-condensation. *Podocarpus* and *Allanblackia* are both quoted, but in Usambara they do not occur together. Also the statement (p. 368) concerning the Upper Tropical that "the atmosphere is drier and warmer" presumably in comparison with the preceding type, is directly at variance with Usambara conditions.

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(3) *Formations without trees.*

(a) Heath = "Heideformationen" of Engler (pp. 327, 331).

(b) Tall Grassland = "Offene Hochgrassteppen" (Engler, p. 273).

(c) Short Grassland of Phillips, 1931, p. 369 = "Trockeneres Weideland" (Engler, p. 331).

(d) Swamp.

N.B. 3 (b) and 3 (c) are subdivisions of the "Grassland" of Tansley and Chipp (p. 206).

(4) *Crop and succession communities.*

See pp. 30-37 below.

DISTRIBUTION OF COMMUNITIES.

The dominant botanical feature of the Usambara Mountains as a whole is their magnificent evergreen forest, which occurs in one form and another throughout, from 500 to 7500 ft. Originally forest appears to have occupied almost the whole of the plateaux, and the Humid south and east scarps of the East Usambaras, but not the other scarps in the Lowland Zone, which are Semi-humid or Semi-arid. There is no sign of the bamboo belt met with on many East African mountains.

At the present day these Usambara evergreen forests are widely separated from any others (see Map in *J. Ecol.* 1933, p. 421). As one descends the mountains in any direction the vegetation changes abruptly. At the bottom of the scarps Savannah or Thorn Country prevails, even in the direction of the Indian Ocean. Generally, the vegetation on the scarps is such that there is a complete break between the arborescent growth at the top and that at the bottom. Thus on the western edge of the West Usambaras the "Cedar" Forest stops abruptly at the edge of the plateau, divided by more than 4000 ft. of bare scarp from the Thorn Country of the Mkomasi Valley. In places the gullies seaming the scarp provide a narrow corridor more or less from the forest at the top to the Savannah at the bottom. Only on the south and east face of the East Usambaras is any extensive area of Lowland Forest connected on a broad front with the forest on the plateau. On those scarps, owing to the pitch of the ground and the scanty soil, the forest is somewhat poorer than it is elsewhere, but the characteristics of an evergreen forest community and its appropriate habitats are maintained without interruption.

A great deal of Evergreen Forest has been swept away in comparatively recent years by human agency, especially since the advent of European settlers fifty years ago. The Lowland and the Intermediate Dry Evergreen Forests have suffered particularly. The Lowland Forest that in 1880 extended as far east as Muhesa has mainly been replaced by Ceara rubber (*Manihot glazovii* Mull. Arg.), sisal and native crops. Certain areas subsequently abandoned have come to resemble Savannah, a waste of rank grass and stunted corky-barked trees, which the local inhabitants sweep annually with fire. It forms, in fact, a pyro-



Phot. 1. Tall grassland with Gallery Forests at 3000- 3500 ft.



phytic climax, and under present conditions Evergreen Forest cannot re-establish itself. It will be convenient to refer to this as Subclimax Savannah.

The first settlers found the East Usambara plateau an almost unbroken mass of forest except for the Tall Grassland on the ridges overlooking the Lwengera Valley. From 1885 to 1914, successive large clearings were made for coffee cultivation. The destruction of forest by the rapidly increasing native population has been continuous up to 1931, when energetic action was taken to stop it.

The West Usambara plateau has always been a more important native area, with the seat of the Sultani of the Wa-sambara at Vuga. The beautiful Short Grassland pastures met with from 4000 ft. upwards may often be of natural origin, but huge clearings have been made within living memory. East of Lushoto one can now look over mile after mile of cultivation without a tree visible, except at long intervals a solitary *Rauwolfia* or *Albizzia*, relics of the Intermediate Dry Evergreen Forest. It is possible that this same community occupied the comparatively low north-east corner of the West Usambara plateau where Subclimax Savannah is dominant.

Table III.

Zone	Chief climatic types occurring	Principal communities occurring in each climatic type	Distribution of the communities	Approximate area
Lowland	Semi-arid	Thorn Country	Plains north and west of mountains	Continuous with much of Kenya and Tanganyika Territory
		Savannah	Plains south and east of mountains	Continuous with much of Kenya and Tanganyika Territory
	Humid	Evergreen Forest (Lowland)	Vestigial at foot of West Usambara scarps Eastern foothills of East Usambaras Patches in eastern foothills of East Usambaras	Less than 50 sq. miles
		Evergreen Forest (Lowland)		
		Subclimax Savannah		10 sq. miles
Intermediate	Semi-humid	Subclimax Savannah	North-east corner of West Usambaras	Uncertain
		Evergreen Forest (Intermediate Dry)	Centre of West Usambara plateau	Vestiges only
	Humid	Evergreen Forest (Intermediate)	East Usambara plateau and south-east corner of West Usambaras	50* and 30 sq. miles respectively
		Tall Grassland	Western edge of East Usambara plateau	Less than 10 sq. miles
		Short Grassland	Interpenetrating "Cedar" Forest and in fallow	?
Highland	Semi-humid	"Cedar" Forest	Western edge of West Usambara plateau	25 sq. miles
		Evergreen Forest (Highland)	West Usambara plateau	150 sq. miles
	Humid	Evergreen Forest (Highland)	West Usambara plateau	
		Evergreen Scrub (Highland)	North and west of Lushoto	Uncertain; merges into Evergreen Forest (Highland) or Heath
		Heath	Widely separated areas in West Usambara plateau	
				? 20 sq. miles

Assessed by Krueger (1894) as 3 Quadratmeilen (=about 70 sq. miles English). Much clearing has taken place since at date.

BIRD HABITATS AND BIRD COMMUNITIES.

IN THE EVERGREEN FOREST FORMATION.

Before dealing with these communities individually it is desirable to describe the many features they possess in common.

Facies. All the six communities are built up on the same plan. The Lowland, Intermediate and Highland Forests, especially, present much the same facies, and except perhaps to an expert botanist their resemblances are more striking than their differences.

Everywhere a fairly dense shrubby undergrowth and an understorey of small trees covers the ground to a height of 10-30 ft. Out of it rise taller straight-stemmed trees which do not branch till they reach a considerable height, often as much as 100 ft. Generally the tree-tops form an almost continuous canopy raised well above the understorey. Nowhere in the Usambara forests do the tree-tops actually interlock into an inseparable mass as in parts of West Africa (cf. Chipp, 1927). Rather it is the rule here, especially in the most luxuriant forests, that the tops of the trees are disproportionately small for their great height, and the liana growth is in a vertical direction, so that the trees retain their individuality whether viewed from above or below. From the floor of the forest many flecks of sky are visible; shafts of sunlight often reach the ground; and in consequence when the sky is clear the forests are pervaded with a soft green light rather than filled with gloom.

Habitats. The bird population of an evergreen forest falls into three divisions:

(a) Birds feeding on the ground or in the lowest few feet of the undergrowth. Practically all of them nest in the undergrowth, not on the ground.

(b) Birds nesting in the undergrowth and foraging upwards, mainly by way of the lianas, and often to the outer surface of the tree-tops.

(c) Birds that pass their lives in the tree-tops and rarely come nearer the ground.

Thus, with reference to feeding there are three habitats, while with reference to nesting the habitat of class (a) is contained within that of class (b). The threefold division is worth retaining. Ground-stratum and Tree-top Habitats are the obvious names for (a) and (c). Mid-stratum may serve for the third¹.

These three habitats are thus defined in their vertical extension. In their horizontal extension, the Ground-stratum and Mid-stratum Habitats might be subdivided, because a number of species absent from the depths of the forests make an appearance on, or just within, its edges. "Edges" here applies not only to the outside of a block of forest, but also to the openings formed within it by the course of a stream or by the fall of a great tree. However, in

¹ Since writing these pages I have received Chapin's fine Congo study (1932). It is gratifying to find that he also has adopted a threefold habitat division for Evergreen Forest. His names for them are "Ground," "Lower Part of the Trees," "Tree-tops."

listing the birds that occupy each habitat and niche it will suffice to insert the note "(edges)" against those to which it is applicable.

Eco-climates. It is probable that the eco-climates to be expected in an Evergreen Forest Formation (Moreau, 1934) are typically developed in the first four of the Usambara Evergreen Forest Communities, but are modified in the "Cedar" and Scrub Communities. These eco-climates may briefly be re-summarised as follows:

(i) Ground-stratum Eco-climate. Light intensity, except in sunflecks, one-thousandth of that of the open air. Humidity more constantly high, to a slight extent even in the Humid Plus region of the East Usambara plateau. Temperature not significantly different from open air in minima, but about 3–4° C. less in maxima.

(ii) Tree-top Eco-climate. At and near the surface somewhat hotter by day and cooler by night than the standard climate, but to what extent is unknown.

(iii) Mid-stratum Eco-climate represents the transition between (i) and (ii). Birds of this habitat are not strangers to either of the preceding eco-climates but they spend the greater part of their time in conditions approximating to (i).

Botanical features. (i) Except to some extent in the Lowland, the Evergreen Forest Communities undergo hardly any seasonal change in foliage and facies. With the modified exception of the "Cedar" Forest, they all provide a perennial and varied supply of fruit in the tree-tops, but comparatively little in the undergrowth, except on the edges.

(ii) There is much dark green undergrowth of a shrubby nature, mainly Rubiaceae and Acanthaceae. They are of a slender branching habit. The cradle-nests and the bag-nests are hung on the horizontal twigs. The cup-nests are built round forks or thrust into coppice growth. The more open spots on the ground are covered with herbs.

(iii) Lianas and creepers are everywhere prominent. In the taller forest they provide the chief means of communication between the tree-tops and the undergrowth. Some of them (e.g. *Ficus* spp.) are the means of attracting frugivorous birds of the Tree-top Habitat nearer to the ground.

(iv) The forest edges are distinguished from the interior by so dense a growth of creepers, e.g. Passifloraceae, Cucurbitaceae, Ampelidaceae, and of rampant and scandent plants, such as *Rubus* spp., that it is usually difficult to enter a forest except by a recognised path. On the edges, moreover, the Ground-stratum is rich in herbs and grasses. The latter especially are the source of essential food and nesting material for forest birds.

(v) The forests are remarkable for their wealth of diverse nesting material; and the nature of the fibres available makes possible the peculiarity of the nest architecture. Its characteristic is an astonishing combination of laciness and strength, unknown in the Palaearctic Region. The lower plants are of special importance in this nest-building economy. A fibre like horsehair appears in a

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great variety of nests, and is the staple especially of the numerous Pycnonotidae and sunbirds (*Cyanomitra* and *Anthreptes* spp.). It consists of the rhizomorphic strands of *Marasmius* spp., which abound throughout the Evergreen Forests. Beard lichen (*Usnea longissima* Ach.) also makes a frequent appearance in nests: it forms the exclusive material of such diverse birds as *Oriolus chlorocephalus*, *Campephaga flava*, *Psolidoprocne holomelaena massaica*. Soft green moss, one species of which produces threads like frayed silk a foot long, is the staple of *Artisornis metopias* and several fly-catchers.

The higher plants of special importance in nest building are those with corkscrew tendrils (climbers)¹ and those with long stringy inflorescences (e.g. *Acalypha Engleri* Pax and *Boehmeria platyphylla* Don).

(vi) A high degree of leaf skeletonisation is a feature of all the Evergreen Forests. Some species of birds use skeletonised leaves so exclusively in their nests that one might believe they could not build at all without them. Such are *Illadopsis s. stictigula* and *Sheppardia cyornithopsis bangsi*, which moreover spend their lives turning over dead leaves in search of insects. Other birds use skeletonised leaves as linings, e.g. *Cryptospiza reichenowi ocularis*. In the last stage of the breakdown of the larger leaves the strongest veins are left separate and are used as fibres in that form.

With the features common to most of the Evergreen Forest thus briefly indicated, each community and its bird population can now be particularised.

Lowland Evergreen Forest Community.

Compared with the Humid plateau forests the Lowland has a somewhat lighter and more uneven canopy. Engler's lists of species are not applicable to much of the surviving Lowland Evergreen Forest. That which he refers to as "oberhalb Muhesa bei Longusa" (foot of p. 289) has practically all been destroyed. In the canopy of the surviving forest *Antiaris usambarensis* Engl., *Ficus* spp., *Sterculia appendiculata* K. Sch., *Trema guineensis* Ficalho, *Chlorophora excelsa* Benth. and Hook. f., and *Albizia* spp. are prominent. All but the last provide fruit for birds, and so do *Sapium ellipticum* Pax, *Sorindeia obtusifoliata* Engl., *Cussonia* sp., and *Canthium* spp., among others.

The undergrowth in this forest tends to be harsh and thorny. A peculiar feature of it is the grass *Olyra latifolia* L. growing like a miniature bamboo in thickets several feet high. It bears a hard seed like a large millet which is an important bird food. Herbaceous vegetation, including grasses of the usual type, is practically absent except on the edges where the rank tropical grasses, presently to be considered, grow densely.

Lianas are numerous, especially *Landolphia* spp. and Ampelidaceae, but ferns and epiphytes are much less abundant than in the Humid Evergreen

¹ At Amani the common forest weaver, *Ploceus bicolor kersteni*, has been found building exclusively with the tendrils of a *Cissus*, whereas in Zanzibar birds of this species use fibres—(Vaughan, *Ibis*, 1930).



Phot. 3. Intermediate Forest at 3000 ft.; seen from above.



Phot. 4. A native clearing with Cassava, bananas and young coco-palms.
Unbroken Intermediate Forest in the background.

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Forests. Neither beard lichen, *Usnea longissima* Ach., nor moss is obvious to the human observer, although the birds resident there are able to find them for their nests.

Birds of the Tree-tops.

Birds of mixed diet:

- Lophoceros melanoleucus (fruit and insects).
- Oriolus chlorocephalus (fruit, insects, flowers).
- Antheptes longuemarei neglectus (insects and flower juices).

Carnivorous birds:

- Hieraetus ayresi.
- Circæetus fasciolatus.

Insectivorous birds¹:

In tree foliage:

- Chrysococcyx cupreus intermedius.
- Apaloderma narina littoralis.
- Indicator v. variegatus.
- Campephaga flava.

Insectivorous birds (cont.):

- Coracina caesia pura.
- Sigmodus scopifrons kirkii.

On the wing:

- Batis mixta.
- Bias musicus changamwensis.

Frugivorous birds:

- Vinago w. wakefieldii.
- Turacus fischeri.
- Bycanistes bucinator.
- Buccanodon leucotis kilimense.
- B. o. olivaceum.
- Viduidibucco simplex.
- Lamprocolius corruseus mandanus.

Birds of the Mid-stratum.

Birds of mixed diet:

- Cyanomitra olivacea olivacina (insects and flower juices).

Insectivorous birds:

In foliage:

- Ceuthmochares aereus australis.
- Chloropetella holochlorus suahelicus.
- Suaheliornis kretschmeri (edges).
- Phyllastrephus flavostriatus tenuirostris.
- P. debilis rabai.
- P. terrestris suahelicus (edges).
- Apalis m. melanocephala.
- Telephorus quadricolor intercedens (edges).
- Nicator chloris gularis.
- Ploceus bicolor kersteni.

Insectivorous birds (cont.):

In bark:

- Campethera c. cailliautii.
- C. abingoni mombassica.
- Dendropicus lafresnayi hartlaubii.

On the wing:

- Dioptrornis fischeri amani.
- Hyloti australis usambara (edges).
- Trocoercus bivittatus.
- Tchitrea viridis².
- Dicrurus l. ludwigii.

Frugivorous birds:

- Eurillas v. virens (edges).
- Chlorocichla flaviventris (edges).

Birds of the Ground-stratum.

Birds of mixed diet:

- Guttera pucherani (seeds, insects, berries).
- Francolinus squamatus usambarae (seeds, insects, on edges only).

Insectivorous birds:

- Cossypha natalensis.
- Illadopsis rufipennis distans.

Insectivorous birds (cont.):

- Neocossyphus r. rufus.
- Erythropygia barbata rovumae.

Seed-eating birds:

- Spermophaga ruficapilla cana.
- Mandingoa nitidula chubbi (edges).

Intermediate Evergreen Forest Community

This is the most luxuriant type of forest existing in East Africa. It occurs only with a fully Humid climate on the seaward slopes of the Usambara, Nguru and Uluguru Mountains, possesses numerous endemic plants and is exceedingly rich in species, the enumeration of which occupies pp. 296-323 of Engler (1910). Dominants cannot be designated in the profusion, but among the many tree species represented *Macaranga usambarensis* Pax and K. Hoffm., *Allanblackia Stuhlmannii* Engl., *Piptadenia Buchananii* Baker, *Myrianthus arboreus* P.

¹ The word "Insectivorous" is taken as covering all kinds of invertebrate animal food.

² Usambara Forest strain, without white in wings (see *Ibis*, 1933, p. 8).

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Beauv., *Berlinia Scheffleri* Harms, and *Parinaria* spp. may be mentioned as important. Tree ferns (*Cyathea usambarensis* Hiern) are prominent.

The trees are loaded with an immense variety of epiphytes—ferns, mosses, *Rhipsalis cassytha* Gaertn., beard lichen and several mistletoes (*Loranthus* spp. and *Viscum* spp.). Moreover they are hung thickly with lianas¹ up to a foot in diameter. There are, too, a number of strangling figs, destined ultimately to become self-supporting forest giants, which send down bundles of aerial roots.

The more open spots bear grass and herbs, especially Piperaceae and Balsamaceae. The latter family provides the only conspicuous ground flower of the forest, *Impatiens walleriana* Hook. f., which displays lovely banks of red blossoms.

The principal grasses are soft low-growing *Panicum* spp., especially *P. brevifolium* L., and *Setaria Chevaleri* Stapf and Hubbard. *Olyra latifolia* L. is not nearly so abundant as in the Lowland Forest.

Among the plants bearing edible berries *Macaranga usambarensis* Pax and K. Hoffm.², *Ficus* spp., *Rauwolfia inebrians* K. Schum., *Canthium* spp., *Sapium ellipticum* Pax, *Rhipsalis cassytha* Gaertn., *Phialodiscus zambesianus* Radlk., and the mistletoes may be cited. They all belong to the upper part of the forest. The staple food of the seed-eaters is provided by the *Setaria* and the *Olyra*.

In addition to the nesting sites and nesting material provided throughout the Evergreen Forests, as already described, reference must be made to certain specialties of the Intermediate Forest. The heads of the tree ferns and of the "forest papaw," *Cylicomorpha parviflora* Urb., are favourite nesting sites, especially of *Cryptospiza*. It is to be noted that these are practically the only two tree growths with prickly stems in this forest. *Bradypterus usambarae* builds chiefly in the heads of the little forest *Pleomele* 3 or 4 ft. high, and also uses their dead leaves. The delicate heads of the forest *Panicum* are employed in nest linings.

Mention may be made here of the palm-like *Dracaena*, *Pleomele papahu* N.E.Br., although it belongs only to the forest edges. Its leaves are the favourite nesting site of the little grey palm-swift (*Tachynautes parvus myochrous*) in the Intermediate Zone.

Birds of the Tree-tops.

Birds of mixed diet:

- Oriolus chlorocephalus*.
- Anthreptes longuemarei neglectus*.
- A. tephrolaema usambarae* (berries and flower-juices).

Carnivorous birds:

- Circaetus fasciolatus*.
- Buteo rufofuscus augur*.
- Accipiter melanoleucos*.

Insectivorous birds:

- In tree foliage:*
- Cercococcyx montanus*.
- Chrysococcyx cupreus intermedius*.
- Heterotrogon v. vittatum*.
- Indicator v. variegatus*.
- Prodotiscus insignis ellenbecki*.
- Campephaga flava*.
- Coracina caesia pura*.

¹ Especially *Canthium* spp., *Strychnos* spp., and *Mussaenda arcuata* Poir.

² The following varied birds have been noted feeding simultaneously on the little green berries of the *Macaranga*: *Buccanodon o. olivaceum*, *B. leucotis kilimensis*, *Zosterops virens usambarae*, *Eurillas v. virens*, *Arizelocichla milanjensis striifacies*, *A. masukuensis roehli*, *Onychognathus w. walleri*, *Anthreptes tephrolaema usambarae*—four "bulbuls," two barbets, a white-eye, a starling and a sunbird.

Insectivorous birds (cont.):

Chlorophoneus rubiginosus.
C. n. nigrifrons.
C. nigrescens.
Ploceus nicolli.

On the wing:

Batis mixta.

Frugivorous birds:

Turturoena delegorguei sharpei.
Vinago w. wakefieldii.
Turacus fischeri.

Frugivorous birds (cont.):

Bycanistes cristatus.
Buccanodon leucotis kilimense.
B. o. olivaceum.
Viridibucco simplex.
Lamprocolius corruscens mandanus.
Onychognathus morio shelleyi (but nesting in rocks).
O. w. walleri.
Stilbopsar kenricki.
Zosterops virens usambarae.

*Birds of the Mid-stratum.**Birds of mixed diet:*

Cyanomitra olivacea olivacina.
Turdus olivaceus roehli (fruit and insects; also on the ground).

*Insectivorous birds:**In foliage:*

Ceuthmochares aereus australis.
Suaheliornis kretschmeri (edges).
Phyllastrephus flavostriatus tenuirostris.
P. debilis albigula.
P. fischeri placidus.
Seicercus ruficapilla minulla.
Apalis m. melanocephala.
A. moreaui.
Artisornis metopias.
Dierurus l. ludwigii.
Nicator chloris gularis.

Insectivorous birds (cont.):

Ploceus bicolor kersteni.

On the wing:

Tchitreia viridis (Usambara forest strain).
Trococercus a. albonotatus.
Smithornis capensis medianus.
Dierurus l. ludwigii.
Alseonax minimus roehli (edges).

In bark:

Mesopicos griseocephalus kilimensis.
Campethera abingoni mombassica.
Dendropicos hartlaubii lafresnayi.

Frugivorous birds:

Arizelocichla milanensis striifacies (edges).
A. masukuensis roehli.
Eurillas v. virens (edges).

*Birds of the Ground-stratum.**Birds of mixed diet:*

Geokichla gurneyi usambarae (fruits and insects).

Insectivorous birds:

Bradypterus usambarae (edges).
Illadopsis rufipennis distans.
I. s. stictigula.

Insectivorous birds (cont.):

Sheppardia cyornithopsis bangsi.
Alethe fulliborni usambarae.

Seed-eating birds:

Spermophaga ruficapilla cana.
Cryptospiza reichenowi sanguinolenta.
Mandingoa nitidula chubbi (edges).

Intermediate Dry Evergreen Forest Community.

This is a lower, poorer, and less completely closed forest community than those previously considered. Fruit is again amply supplied, especially by *Rauwolfia obliquinervis* Stapf, *Ficus* spp. and *Harungana madagascariensis* Lam. The scarlet flowers of the frequent *Erythrina tomentosa* R.Br. possess a special attraction for sunbirds.

As has already been mentioned this forest community has been more completely cleared than any other. I personally have only been able to examine vestigial patches, from which I conclude that its bird fauna is an attenuated form of that of the more luxuriant Intermediate Evergreen Forest. One or two species from the Highland Evergreen Forest make an appearance, but the most prominent of these, *Columba a. arquatrix*, is probably only seasonal, when the *Rauwolfia* is fruiting.

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Highland Evergreen Forest Community.

In general this forest is most like the Intermediate Evergreen Forest, although the specific composition is different, and where the Highland Evergreen Forest occurs in the Semi-humid area it is naturally less luxuriant. I have been particularly struck by the superficial resemblance between the Shagai Forest (6000–7500 ft.) in the extreme north-west corner of the West Usambara plateau, and the Intermediate Evergreen Forest at Amani. Generically, indeed, if not specifically, the Highland Evergreen Forest is closer to the Knysna Forest of the Cape Province (cf. Phillips, 1931*b*) in latitude 23° S., a fact that is of interest in view of the species of birds common to both.

Engler's treatment of this important forest (1910, p. 336) is unsatisfactory. It is supplemented here by particulars based largely upon information given by Mr L. Wigg of the Tanganyika Forests Department.

While naturally there is local variation within the large area covered by this forest, the most generally characteristic of the tall trees are *Podocarpus* spp. and *Ocotea usambarensis* Engl., either separately or in association¹. The fruits of the latter provide a practically perennial source of food. In places on the (Humid) eastern side *Allanblackia Stuhlmannii* Engl. is an important constituent, but not in association with *Podocarpus*. Local subdominants among the canopy trees are *Syzygium* spp. (flowers eaten by several birds), *Pygeum africanum* Hook. f., *Olea* sp., *Chrysophyllum* sp., *Ficus* spp., *Cassipourea Eickii* Alston (all producing edible fruits) and *Ficalhoa laurifolia* Hiern. Other fruit-bearing trees are *Macaranga usambarensis* Pax and K. Hoffm., *Clausena* sp., *Celtis Kraussiana* Bernh. Lianas and epiphytes are fairly numerous. Grasses are inconspicuous and the important *Olyra* of the lower altitude forests is absent.

Birds of the Tree-tops.

Birds of mixed diet:

Anthreptes tephrolaema rubritorques
(berries, flower-juices).

Carnivorous birds:

Stephanoaetus coronatus.
Buteo rufofuscus augur.
Astur tachiro sparsimfasciatus.

Insectivorous birds:

In tree foliage:

Cercococcyx m. montanus.
Chrysococcyx cupreus intermedius.
Heterotrogon v. vittatum.
Indicator v. variegatus.
Coracina caesia pura.
Chlorophoneus rubiginosus.
C. n. nigrifrons.

Insectivorous birds (cont.):

On the wing:

Batis mixta.

Frugivorous birds:

Columba a. arquatrix.
Turturoena delegorguei sharpei.
Turacus hartlaubi.
Bycanistes cristatus.
Buccanodon leucotis kilimense.
Viridibucco simplex.
Pholia sharpii.
Onychognathus w. walleri.
O. morio shelleyi.
Stilbopsar kenricki.
Zosterops virens usambarae.

¹ *Podocarpus* is unknown on the East Usambara plateau, but a close stand of stunted trees covers a few dozen acres between 3200 and 3600 ft. on the extreme tip of a conical peak of Mt Mlinga. No birds of the Highland Evergreen Forest are present there.

*Birds of the Mid-stratum.**Birds of mixed diet:*

- Turdus olivaceus roehli* (insects and berries).
- Cinnerys mediocris usambaricus* (insects and flower-juices).
- Pseudoalcippe abyssinicus* (berries and some insects).

*Insectivorous birds:**In foliage:*

- Phyllastrephus debilis albigula*.
- P. fischeri placidus*.
- Seicercus ruficapilla minulla*.
- Apalis thoracica griseiceps*.
- A. m. melanocephala*.
- Artisornis metopias*.

Insectivorous birds (cont.):

- Laniarius fülleborni*.

On the wing:

- Trococercus albonotatus*.
- Tchitrea viridis* (Usambara Forest strain).
- Dicrurus l. ludwigii*.
- Alseonax minimus roehli* (edges).

In bark:

- Mesopicos griseocephalus kilimensis*.

Frugivorous birds:

- Arizelocichla nigriceps percevali*.
- A. milanjensis striifacies* (edges).
- A. masukuensis roehli*.

*Birds of the Ground-stratum.**Birds of mixed diet:*

- Francolinus squamatus usambarae* (seeds, insects on edges).
- Aplopelia l. larvata* (insects, berries).
- Geokichla gurneyi usambarae* (insects and berries).

Insectivorous birds:

- Illadopsis s. stictigula*.
- Sheppardia cyornithopsis bangsi*.

Insectivorous birds (cont.):

- Pogonocichla stellata orientalis*.
- Alethe fülleborni usambarae*.
- A. anomala montana*.
- Bradypterus usambarae*.

Seed-eating birds:

- Cryptospiza reichenowi sanguinolenta*.
- Linurgus k. kilimensis*.

"Cedar" Forest Community.

This differs in general appearance from the Evergreen Forests we have up to now been dealing with. Instead of presenting a mass of rich greenery and a closed canopy high above the ground, the "Cedar" Forest consists of a tangled mass of vegetation up to about 15 ft. in height with individual *Juniperus procera* Hochst., sometimes over 100 ft. tall, thrusting up through it. There is no closed canopy, and since, moreover, the foliage of the *Juniperus* consists only of needles, the typical Evergreen Forest Eco-climate may not be developed. The light intensity in "Cedar" Forest is not so low, the shrubby and herbaceous vegetation and the epiphytes are much reduced. Balsams and tree ferns are absent.

In species this community is much the poorest. The *Juniperus* produces edible fruit and *Olea hochstetteri* Baker, the principal tree occurring in association with it, attracts great numbers of pigeons at fruiting time. The undergrowth consists largely of *Berberis Holstii* Engl., *Rhamnus Holstii*, Engl., *Myrsine africana* L., *Mostuea africana* Gilg.

In view of the striking differences from the adjacent Highland Evergreen Forest it might have been supposed that the "Cedar" Forest would possess a peculiar avifauna. On the contrary, most species are common to both, and the "Cedar" possesses no peculiar forms. A surprising feature is the reappearance on its outskirts of several species most typically associated with the Lowland Zone generally, rather than with the Evergreen Forest Formation at any altitude—*Lophoceros melanoleucos*, *Oena capensis*, *Dicrurus adsimilis divaricatus*, *Sigmodus retzii graculinus*, *Uraeginthus bengala*.

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Highland Evergreen Scrub Community.

There is some doubt whether this is a climax community or a stage in the regeneration of Highland Evergreen Forest. It often merges into that forest and is interpenetrated by glades of the Short Grassland, especially in the Wambugu cattle country.

It differs from the luxuriant forests first considered in the same direction as does the "Cedar" Community, and to a stronger degree. The scrub consists of a dense mass up to about 20 ft. high, comprising a large variety of bushes and small trees (see Engler, p. 328). A few larger trees are present, e.g. *Mimusops Eickii* Engl., *Trema guineensis* var. *Hochstetteri* Engl., *Agauria salicifolia* Hook. f. (all fruit-producing). The canopy that conditions the typical Evergreen Forest Eco-climate does not exist, and it appears that the typical Bush Eco-climate must be developed in the mass of scrub. This means that in its upper part the climate will be more extreme than the "general" climate, hotter by day and colder by night, but to what extent we do not know; while close to the ground in the shade of the scrub something approaching the equable Evergreen Forest Eco-climate may possibly rule.

This stunted community produces a variety of fruit. A surprisingly large proportion of the Highland Evergreen Forest birds are present, especially considering that owing to the scarcity of large trees nesting sites for hole-dwellers are few.

IN THE DECIDUOUS PARKLAND FORMATION.

This differs from the Evergreen Forest Formation in several respects. The trees characteristic of Parkland are small and never so close together as to form a closed canopy at any season. They are almost wholly deciduous and consequently the formation shows very marked seasonal changes. For our present purpose only two divisions of the great Parkland Formation are recognised, namely, Savannah with thick grass cover and Thorn Country.

Savannah.

The species of trees may vary considerably. A constant feature is a dense stand of grasses of predominantly upright growth and usually from 3 to 6 ft. high. Periodically this is burnt, leaving wide areas of naked blackened ground. Other herbage is relatively unimportant. Bushes are few and far between: where they do occur they tend locally to form dense fire-resistant evergreen masses from 6 to 15 ft. high.

Four habitats can be distinguished in the Savannah, the Tree, Bush, Grass and Ground Habitats. Many of the birds allocated to the Tree Community in the following list find the bulk of their food on the ground, but tree growth appears to be essential for their nesting.

The variety of fruit-bearing plants present in any one place does not seem to be large, and it is not obvious how a perennial supply is secured by frugivorous birds. However, important fruit trees are *Ficus* spp., *Annona senegalensis* Pers., *Bridelia micrantha* Baill., and *Commiphora* spp.

The grass flora varies much from place to place. *Andropogon*, *Pennisetum* and *Hyparrhenia* spp. are widespread; in more humid areas *Panicum maximum* L., *P. infestum* Anders, *Rotboellia exaltata* L., and *Sorghum verticilliflorum* Stapf especially. The lower part of the Usambara scarps and the Sub-climax Savannah that occupies old clearings on the (Humid) seaward slopes of the East Usambara plateau are characterised by these latter grasses. Their seeds apparently vary widely in their palatability to birds, and specific preferences could probably be established. Some of the strongest stemmed grasses provide nesting-sites—e.g. for the Bishop Birds, *Euplectes* spp. and *Melocichla mentalis orientalis*, besides the Cisticolae. *Imperata cylindrica* L., with its fluffy seed-head like that of the familiar "Bog-cotton" provides a nest-lining, especially for Cisticolae and sunbirds.

Between 1500 and 3000 ft., according to locality, the particularly rank and harsh grasses of the Lowland Zone cease to be dominant and are replaced by mat-forming species.

The respective eco-climates may be sketched as follows:

(i) *Tree Eco-climate*. Where the trees stand separate and especially during the long period when they are devoid of leaves, it is possible that this eco-climate may approach the standard climate.

(ii) *Bush Habitat*. Inside unshaded bushes the air temperature tends to be more extreme than the standard. The day maxima may be as much as 5° C. hotter and the night minima nearly as many degrees colder (recorded by Mr T. W. Kirkpatrick, Entomologist at this Research Station, in coffee bushes).

(iii) *Grass Habitat*. The interior of grass-stands of all types is more extreme than the standard climate. As a rule the grass in which birds actually build their nests is of the vertically-growing type, not a mat grass. Standing corn is of similar habit, and between the stems in a European corn-field Geiger (1927) found that the temperature was 4° C. hotter by day and a little lower than the standard at night. When the grass dries up and turns yellow in the hot season the extreme nature of the eco-climate is exaggerated.

(iv) *Ground Habitat*. The eco-climate inhabited by a ground bird is one of the following:

(a) That of the base of vertical grass-stems, which Geiger found in a corn-field to be somewhat more extreme than the standard.

(b) That conditioned by mat grass, where surprisingly high day temperatures have been recorded, especially when the grass is dead. An inch above a grass mulch the temperature may run at least 12° C. higher than the standard. In such a situation 46.5° C. has been recorded at Amani compared with only 30.5° at about 4 ft. over the same spot).

(c) The eco-climate over bare ground. There the maxima may run 4–7° C. above the standard.

The following lists of birds are confined to forms actually met with round the mountains, but for the Savannah no attempt has been made to recognise

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community, as distinct from habitat, subdivisions as in the case of the Evergreen Forest Formation. It does not follow, therefore, that all the birds listed occur together, although many of them do so. It should, however, be said that the Subclimax Savannah occupying old cultivation appears to be far poorer in species than the natural climax Savannah. Contributing causes are the practical absence of the Bush Habitat, and the time factor. The few birds common in the Subclimax Savannah are marked (*).

Tree Habitat.

Birds of mixed diet:

Lophoceros melanoleucos (fruit and insects).

*Cinnyris bifasciatus microrhynchus.

*Chalcomitra amythestina kirkii.

*C. senegalensis aequatorialis.

Anthreptes collaris elachior (flower-juices and insects).

*Pycnonotus tricolor micrus.

Oriolus auratus notatus.

O. monacha reichenowi (insects and fruit).

Carnivorous birds:

Kaupifalco monogrammicus meridionalis.

Terathopius ecaudatus.

Melierax sp.

Insectivorous birds:

In foliage:

Indicator indicator.

Eremomela scotops occipitalis.

Campephaga flava.

Coracina pectoralis.

Sigmodus retzii graculinus.

Chlorophoneus sulphureopectus similis.

Dryoscopus cubla hamatus.

In bark:

Rhinopomastus cyanomelas schalowi.

Phoeniculus purpureus marwitzi.

Campethera nubica scriptoricauda.

Halcyon c. chelicuti (ground-feeding).

Insectivorous birds (cont.):

On the wing:

Coracias c. caudatus.

Eurystomus afer suahelicus.

Merops n. nubicus.

Aerops albicollis major.

Batis molitor soror.

Bradornis pallidus subalaris.

Bias musicus changamwensis.

*Dicrurus adsimilis divaricatus.

Frugivorous birds:

Poicephalus meyeri matschei.

P. fuscicapillus.

Lybius torquatus irroratus.

Pogoniulus pusillus affinis.

Trachyphonus vaillantii suahelicus.

Cinnyricinclus leucogaster.

Lamprocolius chloropterus elizabeth.

Seed-eating birds (largely ground-feeding):

Streptopelia s. semitorquata.

S. capicola somalica.

Anaplectes melanotis.

Quelea spp.

Lagonosticta senegala hildebrandtii.

Uraeginthus bengalus.

*Serinus m. mozambicus.

Spermestes spp.

Bush Habitat.

Insectivorous birds:

*Centropus superciliosus.

Argya rubiginosa heuglini.

Phyllastrephus terrestris suahelicus.

P. strepitans.

Cossypha heuglini intermedia.

Insectivorous birds (cont.):

Laniarius ferrugineus sublacteus.

Tchagra senegala.

Frugivorous birds:

Colius striatus mombassicus.

Andropadus i. insularis.

Grass Habitat.

Insectivorous birds:

Cisticola cheniana heterophrys.

C. natalensis valida.

C. brachyptera reichenowi.

Prinia mistacea tenella.

Melocichla mentalis orientalis.

Seed-eating birds:

Euplectes hordacea changamwensis.

*Euplectes capensis xanthomelas.

Vidua macroura.

Estrilda rhodopygia centralis.

E. astrild.

Ground Habitat.

Birds of mixed diet:

Francolinus sephaena rovuma.

F. hildebrandtii.

Pternistes afer.

Coturnix delegorguei.

Numida m. mitrata.

Birds of mixed diet (cont.):

Lissotis melanogaster.

Mirafra f. fischeri.

Insectivorous birds:

Bucconus cafer.

Caprimulgus fossii mossambicus.

Thorn Country.

Almost all the vegetation in this semi-arid country is thorny. The predominant colour of the vegetation is grey, not green, and it usually looks half-dead. The foliage of the dominant trees, *Acacia* spp., *Commiphora* spp., *Grewia* spp., *Zizyphus* spp., is all light, casting no thick shade. There is great poverty of herbaceous vegetation. Shady bush cover and grass, except occasional detached clumps, are absent.

Only two habitats need be distinguished, the Tree and the Ground. The former includes all the thorny vegetation, and many of the birds nesting there find their food on the ground below. Fruit is provided by the last three of the four prominent tree genera named above. There is nothing to guide us in estimating the nature of the Tree Habitat Eco-climate in Thorn Country. The Ground Eco-climate, where conditioned by the bare soil, will be extreme, as mentioned under Savannah.

To some extent the Thorn Country shares the Savannah avifauna. Round the Usambara Mountains, however, the species listed below appear to be characteristic of Thorn Country.

*Tree Habitat.**Birds of mixed diet :*

Turtur senegalensis.
Lophoceros deckeni.
Spreo fischeri.
S. hildebrandti.
Ploceus intermedius.

*Insectivorous birds :**In foliage :*

Laniarius funebris.
Rhodophoneus cathemagenus.
Eurocephalus ruepelli.
Calamonastes s. simplex.
Apalis rufifrons rufidorsalis.
Anthoscopus caroli rothschildi.
Erythropgia leucoptera vulpina.
Macronyx aurantiigula.
Perissornis carunculata.
Sylvietta brachyura leucopsis.
Parisoma b. böhmi.
Parus afer barakae.
Dryoscopus pringlii.
Nilais minor massaicus.
Pseudonigrita cabanisi.

In bark :

Rhinopomastus cabanisi.
Campethera nubica pallida.
Dendropicos fuscescens massaicus.

On the wing :

Batis minor subsp.
Bradornis griseus.

Frugivorous birds :

Colius macrourus pulcher.
Trachyphonus d'arnaudi boehmi.
Tricholaema melanocephalum stigmatothorax.
Lybius melanopterus.
Corythaixoides leucogaster.
Poicephalus rufiventris.

Seed-eating birds :

Hypocera ultramarina purpurascens.
Lagonosticta senegala somaliensis.
Vidua fischeri.
Pytelia melba.
Uraeginthus cyanocephalus.
Granatina i. ianthinogaster.
Serinus dorsalis taruensis.
Dinemellia dinemelli.

*Ground Habitat.**Birds of mixed diet :*

Aeryllium vulturinum.
Pterocles d. decoratus.
Pternistes leucoscepus infuscatus.
Eremopterix leucopareia.

Mirafr poecilosterna massaica.
Limicolae spp.

Insectivorous birds :

Caprimulgus donaldsoni.

IN FORMATIONS WITHOUT TREES.

Heath Community.

This appears to be typically developed on poor gravelly soil in the Highland Zone. *Philippia* sp. forms with bracken (*Pteridium aquilinum* Kuhn), a dense matted growth from 3 to 5 ft. high, completely hiding the ground. Practically the only other plentiful plant is a yellow-flowered *Smithia* sp. Grass is absent.

It is obvious that this is a one-habitat community providing comparatively little bird food. Judging from Temperate Zone observations (Geiger, 1927) its eco-climate will be hotter by day than the standard climate, except possibly within a few inches of the ground.

The one characteristic bird is *Bradypterus cinnamomeus* (an insect-eater). *Saxicola torquata axillaris* (stonechat) also occurs. Where small trees (especially *Myrica*) invade the Heath they attract other birds, e.g. sunbirds and *Zosterops* sp.

Tall Grassland Community.

This occupies some of the ridges of the East Usambara plateau overlooking the Lwengera Valley. It is intersected with gallery forests derived from the adjacent Intermediate Evergreen Forest. Possibly the Tall Grassland occupies the site of native clearings made at least a century ago and represents a pyrophytic climax. It consists of grasses from 2 to 8 ft. in height growing in distinct clumps. Dominants are *Hyparrhenia rufa* Stapf, *H. variabilis* Stapf, *Themeda triandra* Forsk., and *Cymbopogon* spp. It will be observed that its composition differs both from the "Hochgrassteppe" described by Engler (p. 263) in Kenya and from the Subclimax Savannah on the east face of the East Usambaras (in the Lowland Zone). Typically the Tall Grassland is devoid of trees or bushes. Flowering herbs are often conspicuous¹. There are practically no game or cattle feeding on the grass, which has indeed been ascertained by analysis to be gravely deficient in mineral constituents.

This community resembles the heath in offering practically only a single habitat with a poor supply of food. The eco-climate is again more extreme than the general.

The avifauna is poor but of considerable intrinsic interest. The characteristic birds are a nightjar, *Caprimulgus guttifer*, known only from the Usambara Mountains, *Saxicola torquata axillaris*, *Coliuspasser ardens teitensis* and *Cisticola brachyptera reichenowi*, elsewhere known only from the Lowland Zone. Such species as *Estrilda astrild*, *Euplectes capensis xanthomelas*, *Cisticola natalensis valida*, and *Melocichla mentalis orientalis*, characteristic of the Grass Habitat of the Savannah, are present, but only in very small numbers. Larks and pipits are unrepresented.

Where small trees occur in this community, chiefly on the edges, they are

¹ Especially *Polygala gomesiana* Welw., *Gladiolus quartenianus* A. Rich., *Aristea alata* Baker, *Cassia mimosoides* L. and *Crotalaria* spp. The occasional *Leonotis* spp. are much visited by sunbirds for the flowers and by *Coliuspasser* for the seeds.

of the fire-resistant type (*Erythrina tomentosa* R. Br., *Strychnos* spp., *Ormocarpus* sp., *Vangueria tomentosa* Hochst., and *Syzygium* sp.), not derived from the surrounding Intermediate Evergreen Forest. They are responsible for the appearance of *Lanius collaris humeralis*, *Cinnyris amethystina kirkii* and *Pycnonotus tricolor micrus*.

Short Grassland Community.

This is confined to the Highland Zone (West Usambaras) except for a few hundred acres in the Intermediate east of Lushoto. It occurs in fallow and pasture, and probably more naturally as "rides" where drainage is poor in the Highland Evergreen Scrub and the "Cedar" Forest. Most of its constituent grasses (see Eichinger, 1914) do not appear in the lower zones, while on the other hand the rank grasses of the Savannah and the Tall Grassland are completely absent.

This Short Grassland supports numerous stock to which it must owe in part its beautiful lawn-like texture. But the amount of grass seed produced is apparently small, and it is doubtful whether it is specifically acceptable to birds. The very simplified habitat possesses an extreme eco-climate; besides much higher maxima, 7 and even 10° C. above the standard (T.W.K.), short turf induces abnormally low night minima.

The only characteristic species are *Anthus richardi lacuum* and, sporadically, *Coturnix africana*. The domestic stock bring the oxpecker, *Buphagus erythrorhynchus caffer*. The smallest sprigs that will serve as perches are used by *Lanius collaris humeralis*, which lives on the abundant grasshoppers.

Swamp Communities.

It is a natural consequence of the topography that any swamps in the mountains should not be extensive. Such as there are take the form of narrow strips, due to the retardation of stream-flow through damming or natural silting. As they inhibit forest growth they effect an appreciable gap in the forest shade and always lie open to the sky. Excluding areas with open water, which are dealt with later, two main Swamp communities are distinguished for our purpose:

(a) Rank vegetation up to 10 ft. high, chiefly bulrushes (*Typha australis* Schum. and Thonn.) with a Giant Cyperus or with "Elephant Grass" (*Pennisetum purpureum* Schum.). Found from Lowland to Highland. Two habitats are distinguishable:

(1) At water-level. Characteristic birds, *Limnocorax niger* and *Rallus caerulescens*.

(2) The tops of the rushes, etc., where *Bradypterus brachypterus moreau*, *Calamornis leptorhyncha* and *Amblyospiza albifrons unicolor* build.

(b) In a type of Swamp confined to the plateaux the mud is covered with a dense tangle of vegetation only about 3 ft. high. The rank fern *Dryopteris*

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gongylodes O. Ktze is dominant. There is no upstanding vegetation such as provides nesting-sites for the passerine species listed under (2) above. This *Dryopteris* swamp is usually narrow and hemmed in by forest. The characteristic bird is the pygmy rail, *Sarothrura rufa elizabethae*.

IN CROP AREAS.

It may be accepted that in the mountains, and to a great extent in the foothills, all the land under crops was originally covered with forest. Native cultivation is practically all shifting, the same piece of land being cropped for one to three years and then allowed to lie fallow. European agriculture has been chiefly concerned with permanent crops: Ceara rubber (*Manihot glaziovii* Mull. Arg.) in the foothills (Lowland Humid and Semi-humid Zones), coffee (*Coffea arabica* L.) on the plateaux (Intermediate Humid and Highland Semi-humid). Sisal, which covers large areas in the surrounding plains (Lowland Semi-humid), need not concern us here. The plantations belonging to the East African Agricultural Research Station (Intermediate Humid) demand special treatment.

No study has yet been made of the interrelations of birds and crops in East Africa. The question of the bird community associated with a given crop is not a straightforward one because it varies with the maturity of the crop and the amount of attention it receives, especially in the matter of weeding. It is, moreover, a truism that the list of birds frequenting any particular area under crop depends to a great extent on the nature of the immediate surrounding vegetation. The treatment of the subject here is very summary, designed primarily to indicate which birds have shown the adaptability necessary to take advantage of strange foods and strange conditions.

The succession of bird communities as a cultivated area reverts to natural conditions is touched upon separately. A subsection is devoted to exotic weeds that are important to birds or dependent on birds for their dispersal.

The initial clearing is practically always accompanied by burning, whether primary forest is concerned or merely a season's weeds. The immediate result is a bare and blackened soil, which the first rains wash clean. In the mountains it is an exceptional thing to see any bird working bare soil. The only birds ever noted on it are the bunting (*Emberiza major orientalis*) and very occasionally a crow, raven (*Corvus albicollis*), starling (*Lamprocolius corruscus mandanus*), or coucal (*Centropus superciliosus*). In the case of freshly cleared ground it might be supposed that the firing had destroyed the insect food, but the same negative observation applies with equal force, in the mountains at any rate, to permanent cultivation that is kept clean-weeded and to ploughland where firing has not taken place for many years.

In dealing with the fauna of isolated clearings in the forest it requires to be borne in mind that there is a time factor operating. Some of the cleared areas became open to colonisation by non-forest birds only 20 years ago. It is possible that their population will not have reached stability yet. This applies to clear-

ings entirely surrounded by forest more strongly than to those connected by corridors of clearing with a reservoir of non-forest birds. That the process of colonisation is still progressing is evidenced by the arrival of the pied wagtail (*Motacilla vidua aguimp*) in the Amani and Kwamkoro clearings (see Map 2) since 1930. The reality of the barrier presented by Evergreen Forest to non-forest birds is illustrated by the spread of *Lantana camara* L., which is wholly bird-carried (see p. 33).

Annual cultivation.

The staple crop of the Wa-sambara is maize, which flourishes from sea-level up to at least 6500 ft. Apart from any other considerations it is probably too short-lived a crop to provide any nesting sites. In the Lowland Zone the grain, while still small and green, is taken to some extent by the weavers, *Ploceus aureoflavus* and *P. nigriceps*, and the bishop-bird, *Euplectes hordacea changamwensis*. All these birds are absent from the higher zones except *Ploceus aureoflavus* in the Intermediate Semi-humid. The coucal, *Centropus superciliosus*, has been found using the papery dead sheaths as nesting material.

Other native crops in order of area are cassava, bananas, rice and tobacco. None of them is of more than the most trifling importance in avian economy except the rice grown in the Lowland Zone; but this, when it is ripe, attracts great numbers of birds, especially Queleas. The bananas usually harbour no birds, except that occasionally *Ploceus reichenowi* and *P. ocularius suahelicus* lash their nests round the mid-rib of a leaf.

Permanent cultivation.

Ceara rubber. The plantations in the foothills have all been neglected for more than ten years. The trees themselves form a deciduous woodland rather thicker than the densest stand naturally met with in climax Savannah. Thus even in the season of leaf-fall the ground is shaded to some extent, and moreover these areas are not fired. Under present neglect rubber plantations are mostly covered with a thick mat of *Panicum trichocladum* Hack. Undergrowth and saplings of forest species have often begun to appear.

The Tree Habitat approximates to the general climate. The chief birds observed in it are *Bias musicus changamwensis* and sunbirds, especially *Chalcomitra senegalensis*. The rubber trees are not intrinsically attractive. Their hard seeds are probably inedible to every bird, and their bark is smooth. The Ground Habitat will be rather warmer than the "general" climate when the trees overhead are naked. *Guttera pucherani*, the crested guinea-fowl, is a characteristic inhabitant.

Coffee. This has occupied most of the European clearings on the plateaux.

The cultivated coffee bush forms a fairly dense mass of foliage about 6 ft. high. It has been the local practice to provide a light shade by planting "silky oaks" (*Grevillea robusta* A. Cunn.). Old-established plantations present indeed the appearance of groves of *Grevillea* with an undergrowth of coffee. Tree and

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Bush Habitats are thus provided. The bird population depends on the degree of their development and, of course, on the extent to which "clean-weeding" is practised. Newly hoed and planted areas are an ornithological desert.

The Tree Habitat is occupied by *Alseonax minimus roehli*, *Ploceus reichenowi*, *Pycnonotus tricolor micrus*, and the citril, *Spinus citrinelloides hypostictus*. The abundance of the latter depends on the amount of weed seeds available on the ground below. *Oriolus chlorocephalus*, and a starling, *Onychognathus w. walleri*, from the surrounding forests frequent the tree-tops, especially to browse the *Grevillea* flowers in season.

The Bush Habitat possesses one characteristic bird in the bunting, *Emberiza major orientalis*, in the Intermediate Zone plantations but not in the Highland. Estrildinae, a flycatcher, *Batis molitor soror*, and *Tchagra australis* also occasionally build in the coffee bushes. Coffee berries when ripe are sometimes nibbled by colies (*Colius striatus*).

The Amani plantations.

The clearing up the hill to Amani and in the neighbourhood of the Research Station buildings has taken on a highly exotic aspect owing to the establishment, since 1900, of economic plants from all over the tropics. There is every variety of growth, from oil-palms and bamboos to tree-heather, from tea-bushes and the spindly areca palms to the densely dark cinnamon and camphor trees¹. This anomalous area is of special ecological interest for two reasons: (a) because the well-grown tree plantations afford a means of gauging the adaptability of some birds of the surrounding forest; (b) because many of the introduced plants have assumed a position of great importance to the local birds.

Adaptability of forest birds. Some of the introduced trees are very large and they have in places grown so densely that they throw a perennial shade (e.g. camphor and *Callophyllum Inophyllum* L.). But lianas and the characteristic forest undergrowth are absent. It is not then unexpected to find that the birds inhabiting the Ground and Intermediate Strata of the surrounding forest should not have made their home in the plantations. Actually only two have been observed to make, as it were, cautious and selective incursions into plantations. *Suaeliornis kretschmeri* may sometimes be heard calling in the crypt-like groves of the oil-palms: and especially on dull evenings the dense foliage of the cinnamon trees may be full of *Arizelocichla milanjensis striifacies* attracted by the berries.

Why many of the birds of the forest canopy are seen or heard in the plantations but little or not at all, is far from obvious. While some, e.g. *Oriolus chlorocephalus*, *Viridibucco simplex*, starlings and white-eared barbets, *Buccanodon*

¹ The 14 acres of permanent pasture made up of the introduced *Paspalum dilatatum* Pair is of negative interest because the only birds that utilise it at all are those hawking insects on it, viz. two pairs of shrikes, *Lanius collaris humeralis* and two of drongos, *Dicrurus adsimilis divaricatus*. No ground bird occurs.

leucotis kilimense, range freely through the introduced trees in search of food, and make themselves obvious by their cries: others, such as the olive barbet, *Buccanodon o. olivaceum* and insectivorous birds like *Chlorophoneus* spp., the little drongo, *Dicrurus l. ludwigii*, *Apalis melanocephala*, *Ploceus bicolor kersteni*, do not. Their food is not specialised, and since several of the species quoted cling to the smallest vestiges of forest and make an early appearance in the regenerating forest succession, one would suppose that they would find it easy to pass from the forest trees into those of the plantations, which are often contiguous. This point is obviously of importance in the question of range limitation.

Utilisation of introduced plants. This subject is not so complex as the preceding one. The interconnections between the exotic plants and the local birds are many and obvious. A few instances will suffice.

The Widdringtonias and Araucarias provide nesting sites which the local *Spermestinae* favour above all the native growths. Some of the tall introduced palms attract the palm-swifts which otherwise would, in the absence of native palms in the mountains, be entirely dependent on *Dracaenas* (*Pleomele papahu* N.E.Br.). The flowers of *Eucalyptus* spp. are eaten by *Spermestes nigriceps*. Certain trees such as *Jacaranda mimosifolia* D. Don and *Eugenia malaccensis* L. attract great numbers of olive sunbirds, *Cyanomitra olivacea olivacina*. During the six weeks when the *Eugenia* is in flower a single well-grown tree harbours every day from dawn till dark at least a hundred of these birds: yet it does not seem to attract another resident sunbird—*Anthreptes collaris elachior*. The vegetable down of the kapok tree (*Ceiba pentandra* Gaertn.) is used as a nest lining.

The berries of the cinnamon are eagerly devoured, especially by the two starlings, *Lamprocolius corruscus mandanus* and *Onychognathus w. walleri*. White-eared barbets, starlings and colies visit the juniper trees when they are fruiting. The half-wild guava trees, *Psidium Guajava* L., attract the same barbets, geelgats and *Bycanistes cristatus*. These hornbills also swallow the fruits of *Hovenia dulcis* Thunb. and *Maesopsis Eminii* Engl. The latter is a valuable Uganda timber tree that is being disseminated over a radius of several miles from Amani by the birds. Actually, although the plantation is a small one it apparently provides the staple food for about fifty of these great hornbills for six weeks in the year.

Birds and some exotic weeds.

(i) *Lantana camara* L., originally a native of Tropical America, has produced one of the major weed problems elsewhere in the tropics, especially in India and Hawaii. Its small umbels of pink and orange flowers produce a loose cluster of berries each as big as a peppercorn. They are somewhat aromatic and are eaten with avidity by many different birds. The seeds remain highly viable after passage through the avian alimentary canal and they are dependent on this means for their dispersal (cf. Ridley, 1930).

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This *Lantana* appears to have been introduced at Amani some time before 1914. About 1921 it began to spread to an undesirable extent. Owing partly to constant repressive measures, it has not succeeded in establishing itself in the Amani plantations as such a rampant nuisance as in some other tropical countries; but on a neighbouring estate, where less attempt has been made to keep it in check, it has covered abandoned cultivation with impenetrable thickets 7 to 8 ft. high. It must be considered an important source of food for the local birds: sunbirds frequent the flowers; geelgats, colies, barbets, white-eyes (*Zosterops virens usambarae*) and doves (*Tympanistria t. fraseri*) consume the berries, which indeed even attract certain Pycnonotidae out of the forest undergrowth and *Turacus fischeri* from its tree-tops.

It is interesting to observe that the spread of this *Lantana* from the Amani clearing has been up to the present practically confined to areas that are in direct communication by corridors of cleared land. Its hold is strongest on the Nderema clearing, it reaches Bulwa and the bottom of the "Zigi Hill" (see Map 2), but it has so far made practically no appearance in the Kwamkoro clearing. At its nearest point this is less than 2 miles from Amani, but it is surrounded entirely by primary forest. Here we appear to have an indication of the effectiveness of the barrier presented by primary Evergreen Forest to movements of non-forest birds.

(ii) *Clidemia hirta* D. Don. is another American plant that was probably introduced to Amani by accident. It bears quantities of soft purple berries, the seeds of which are distributed by birds. In Fiji it has earned itself the name of "Koster's Curse." According to Dr J. D. Tothill, who as Director of Agriculture, Fiji, knew it well, in the East Usambara generally the edges and waste corners of clearings, and the sides of roads and tracks provide ideal conditions for the plant. At Amani it is interesting to observe that, besides not reaching the same fantastic size as in Fiji, *Clidemia* is making only a comparatively slow advance outwards from Amani along shaded forest tracks. The birds feeding on the berries are species associated with the forest, chiefly *Turdus olivaceus roehli* (the olive thrush) and several Pycnonotidae. The absence of sporadic colonies of *Clidemia* in other Usambara localities, where the conditions for it are equally good, and its slow progressive advance from Amani would argue a sedentary habit for the species eating the fruit. In this connection it is interesting to compare Dr Tothill's remark (*in litt.*) that in Fiji in a comparatively short time *Clidemia* spread to a number of islands up to 30 miles across the sea.

(iii) *Galinsoga parviflora* Cav. is a small Composite that is understood to have been introduced in imported fodder during the East African Campaign. It has established itself over an immense area of East Africa including the Usambaras. The plant is not primarily dependent upon birds for dispersal. It has, however, been observed that its seeds are taken eagerly by *Estrilda astrild*, *Spermestes n. nigriceps* and *Coccygia melanotis kilimensis*.

IN SUCCESSION COMMUNITIES.

For our purposes three subclimax stages may be distinguished in the reversion of crop-land to Evergreen Forest, viz. the Herbage, Bush and Small Tree stages. Ridley (1930, p. 385) has stressed the importance of birds in bringing about the later stages of this succession.

Almost before the harvest is gathered the land has become covered with herbaceous vegetation. Shortly, a bushy growth, which may or may not be destined to grow into forest trees, invades and begins to suppress the herbage. Incidentally it may be mentioned that native clearing is rarely clean except in small patches. In native areas, therefore, bush or tree growth is not usually quite absent at any stage. The eco-climates of both Herbage and Bush stages will be extreme.

Finally the tree flora asserts itself. After a period that is probably nowhere less than ten years a recognisable canopy appears and herbage is almost eliminated. The climbing plants, noted under Evergreen Forest Communities as being particularly characteristic of the forest edges, are abundant. After the land has lain fallow for twenty years the regenerating forest still lacks the characteristic facies, and probably the characteristic equable eco-climate, of the climax. Hardly less than forty years appear to be necessary before these are attained. Forest that on the best (native) information available has been regenerating for sixty years is still obviously secondary.

Herbage stage. In the Lowland Zone the rank tropical grasses become dominant, and the birds of the Savannah Grass Habitat begin to make their appearance. If frequent firing takes place the Subclimax Savannah Community will establish itself.

In the Humid part of the Intermediate Zone, bracken and the mat-grasses *Panicum trichocladum* Hack. and *P. conjugatum* Berg, become locally dominant. *Panicum maximum* Jacq. is plentiful. This provides a favourite food of the numerous Estrildinae, *Spermestes n. nigriceps*, *Amauresthes fringilloides*, *Estrilda astrild*, *Coccygia melanotis kilimensis*, and the delicate seed heads of *Panicum trichocladum* are their staple nesting material. With these grasses a certain amount of herbage shoots up, in which *Prinia mistacea tenella* nests, and *Cisticola erythrops sylvia*, utilising especially the coarse leaves of a *Solanum* sp. The soft orange berries of *Hoslundia opposita* Vahl attract colies and geelgats, *Pycnonotus tricolor micrus*. *Bidens pilosus* L., the "Black Jack," seizes upon spots of bare soil and provides a favourite food of the citril, *Spinus citrinelloides hypostictus*.

In the Highland Zone and also in the Semi-humid area of the Intermediate Zone on the West Usambara plateau¹, the first stage of the fallow is very

¹ For a census of such an area see R. E. and W. M. Moreau (1931). I take the opportunity of correcting certain names. For *Coturnix delegorguei* and *Cinnyris mediocris usambaricus* read *C. africana* and *C. venustus falkensteini* respectively.

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different. No lush herbage, rank grass or mat grass is present. The grass usually forms short turf (see Eichinger, 1914, for lists of species) and the herbage tends to be woody. *Solanum* sp., *Abutilon indicum* Don, *Artemisia afra* Jacq., *Psiadia arabica* Jaub., *Vernonia* spp. and *Leonotis* sp. have been noted as characteristic. The last is important; *Drepanorhynchus reichenowi* is always associated with it, and in a lesser degree *Nectarinia famosa* also. *Poliospiza striolata* and *Prinia mistacea* are the other chief birds of this Herbage stage, with *Anthus richardi lacuum* on the short turf. Cisticolae are almost absent, and the Estrildinae are much less numerous than in the Intermediate Humid.

Bush stage. In the Lowland Zone Humid Type, if the Herbage stage has escaped firing and bushes establish themselves, the birds of the Savannah Grass Habitat are gradually displaced. The following are prominent among their successors, all closely dependent on dense bush growth.

Insectivorous birds:

Camaroptera brevicaudata griseigula.
Heliolais erythroptera rhodoptera.
Laniarius ferrugineus sublacteus.
Tchagra australis.
Cossypha heuglini intermedia.
Centropus superciliosus.
Argya rubiginosa heuglini.
Turdoides jardinei kirki.

Insectivorous birds (cont.):

Nicator chloris gularis.

Frugivorous birds:

Chlorocichla flaviventris.
Andropadus i. insularis.
Colius striatus.

Seed-eating birds:

Hypargos niveoguttatus.

In the Intermediate Zone Humid Type the bushy growth of this second stage of fallow consists mainly of young saplings of forest trees, with the addition of *Harungana madagascariensis* Lam. (fruit-bearing). None of the Intermediate Evergreen Forest birds appear at this stage, except *Bradypterus usambarae*, and then only where the foliage is very dense. The chief species are *Laniarius ferrugineus* sublacteus, *Chloropeta natalensis* massaica, *Cossypha heuglini* intermedia, *Centropus superciliosus*, *Ploceus ocularius* suahelicus, *Antichromus minutus* (all insectivorous), *Colius striatus* and *Pycnonotus tricolor micrus*.

In the Highland and Intermediate Semi-humid Zones the shrubby growth includes such species as *Rumex madarensis* Lowe, *Tephrosia* sp., *Nuxia* sp. It harbours *Cossypha caffra* iolaema, *Argya rubiginosa* heuglini, *Cinnyris venustus falkensteini*, and *Turdoides jardinei* kirki.

Small Tree stage. Generally speaking the birds already noted under Evergreen Forest Communities as belonging to the forest "edges" are those that make their appearance at this stage in the succession. It is probable that nearly fifty years are necessary under the most favourable conditions before the full avifauna of the climax forest is restored.

In the Lowland Zone the pioneer trees of the Evergreen Forest are *Albizzia* spp., *Trema guineensis* Ficalho, *Sorindeia* sp. and *Sapium* sp. All but the first are fruit-bearing. To the birds already noted as belonging to the edges of the forest climax may be added *Pycnonotus tricolor micrus*, *Dryoscopus cubla hamatus* and *Cossypha natalensis*.

In the Intermediate Humid prominent pioneer trees are the very important fruit-bearing *Macaranga usambarensis* Pax and K. Hoffm. and *Trema guineensis* Ficalho, with *Anthocleista orientalis* Gilg and *Cylicomorpha parviflora* Urb., etc. Perhaps the first characteristically forest bird to appear is *Apalis m. melanocephala*, to be followed by the birds noted as belonging to the climax forest edges, by *Ploceus bicolor kersteni* (apparently when lianas have developed) and often *Trococercus albonotatus*.

In the Highland Zone *Agauria salicifolia* Hook. f., *Myrsine africana* L., *Celtis Kraussiana* and *Myrica kilimanscharica* Engl. are pioneers of a succession community approximating to the Highland Evergreen Scrub already referred to. *Apalis thoracica griseiceps*, *Alseonax minimus roehli* and *Zosterops virens usambarae* are about the first of the forest species of birds to make their appearance.

IN HABITATS NOT CONDITIONED BY VEGETATION.

These are of little importance compared with the complex and varied vegetational habitats. They practically fall into the two divisions of habitats conditioned by rocks and by open water respectively.

Rock habitats.

In the Lowland Zone there is comparatively little out-cropping of rocks and there are no cliffs. These are plentiful in the Intermediate and Highland Zones, although the gneiss of which they are composed tends to present smooth faces rather than ledges and crannies. Caves are rare.

Rock outcrops: *Anthus lineiventris*, *Thamnolea cinnamomeiventris usambarae*.

Cliffs: *Micropus apus* subsp., *Ptyonoprogne rufigula*, *Corvultur albicollis*, *Onychognathus morio shelleyi*.

Hirundo abyssinica unitatis and *H. smithii*, which with the dependent *Micropus caffer struebellii* are common on European buildings, belong naturally to the Cliff Habitat.

Open water habitats.

These are divided into Stream and Still-Water Habitats.

Stream Habitat. In the Intermediate and Highland Zones the running water is predominantly clear and torrential; in the Lowland it is more placid and muddy. Bird communities are as follows:

Lowland: *Podica petersi*, *Cuncuma vocifer*, several spp. of Ardeidae, *Ceryle rudis*, *Megaceryle maxima*, *Corythornis c. cristata*, *Phalacrocorax africanus*, *Anhinga rufa*, *Hagedashia hagedash*, *Motacilla vidua aguimp*.

Intermediate: *Alcedo semitorquata*, *Motacilla clara*.

Highland: *Anas sparsa*.

Still-Water Habitat. In the Lowland Zone this is represented in a few small lakes in the Lwengera Valley and near the southern scarp of the mountains.

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In the Intermediate the only still open water is artificial, a few acres in mill-dams. In the Highland there is one natural lake, Manolo, narrow and about 500 yards long, at 6000 ft. in the "Cedar" country. Bird communities are:

Lowland: Practically the Stream Habitat Lowland Community with the addition of *Actophilus africana* and *Thalassornis leuconotus*.

Intermediate: *Poliocephalus ruficollis capensis*.

Highland: *P. r. capensis* and *Anas sparsa*.

ZOOLOGICAL ASSOCIATIONS.

VERTEBRATES.

A number of records of Usambara vertebrates are included in Möbius (1895), but exact identifications rest almost exclusively on Loveridge's collections. The mammals were described by Allen and Loveridge (1927), the cold-blooded vertebrates by Barbour and Loveridge (1928). As Loveridge collected in comparatively few localities, we know authoritatively far too little about the distribution of the non-avian vertebrate fauna. His records can, however, be supplemented by our own observations and by native information. On the whole the zonation of the mammals appears to be less marked than that of the birds, and for the majority of them there is evidence that they range from the Lowland to the Highland throughout. In dealing with them I shall refer to their range only where there is evidence that it is restricted.

Mammals.

"Big game" proper is almost absent from the mountains, although rhinoceros, hippopotamus and elephant occur in the Lwengera Valley, and are resident in the bush of the surrounding lowlands. Lions only very occasionally come up into the mountains, but leopards are not uncommon at all altitudes in and about the forests.

Buffaloes live in some numbers in the lowlands, whence they visit the scarps above the Lwengera Valley. Other herds appear to be permanently resident in the Shume Forest. Cultivation is liable to be overrun with wild pig everywhere except in the very extensive and complete clearings in the middle of the West Usambara plateau. The only other ungulates occurring in the mountains are the following antelopes: *Tragelaphus scriptus massaicus* Neumann, a bush-buck, very common in both forest and cultivation; *Nesotragus m. moschatus* von Duben, a dik-dik, in small numbers in bushy country; *Cephalophus h. harveyi* Thos., the red duiker, in Evergreen Forest throughout; *C. abbotti* and *C. melanorheus schusteri* Matschie, Abbott's and the blue duiker, in the Highland Zone forests.

No direct connection has been traced between the foregoing mammals and any of the birds. The extensive disturbance of the litter and topsoil by the rootings of the wild pig in the forest must, however, be of some importance in the economy of the ground-feeding birds. With the exception mentioned in the

next paragraph, hair has not been noted in any nests. The rarity of vultures in the mountains may well be connected with the scarcity of game in open country.

Only a few cattle are kept, except on the West Usambara plateau where they are numerous, together with sheep, goats, donkeys and pigs. The distribution of the red-billed oxpecker (*Buphagus erythrorhynchus caffer* Stanl.) is, as might be expected, dependent on that of the domestic stock in the absence of big game. The birds are, however, by no means always present in areas where there are plenty of cattle. The practice of dipping tends to eliminate them locally, partly because it destroys their food supply, which is largely ticks (Moreau, 1933), and partly because they are poisoned by picking up arsenic adhering to the hair and hide. Hair from domestic stock provides the staple nesting material of the oxpecker.

Bubulcus ibis (L.), the cattle egret, is another bird constantly found in attendance on cattle at Korogwe (at the mouth of the Lwengera Valley), where meat supplies pass on the hoof from Masailand to the coast. On the plateaux it appears only as a rare straggler.

There are a number of species of smaller mammals that can, either on evidence or on overwhelming presumption, be put down as destructive to bird life, especially in the forests:

Viverridae, several spp.; including *Genetta stuhlmanni* Matschie, *Nandinia binotata arborea* Heller, and the mongooses, *Herpestes galera* Erxl., *Atilax paludinosus rubescens* Hollister, *Bdeogale crassicauda omnivora* Heller, and *Myonax* spp.

Mustelidae; *Mellivora ratel* Sparrm., the honey-badger.

Sciuridae; *Anomalurus orientalis* Peters, which is a flying squirrel; *Heliosciurus u. undulatus* True., *Paraxerus palliatus suahelicus* (Neum.) and *Aethosciurus byatti* Kershaw, the last of which appears to be replaced in the Highland Forests by *Funisciurus vexillarius* Kershaw.

Muridae, several spp. Apart from destroying eggs and nestlings some of the mice take possession of the snug nests of the Estrildine Weavers before they have been occupied.

Lemuridae, at least 2 spp. in the Lowland Zone.

Cercopithecidae. *Cercopithecus pygerythrus johnstoni* Pocock in the Lowland Forest; *C. albigularis rufilatus* Pocock, the "Blue Monkey", in the Forest of all three Zones; and baboons, which are confined to open Lowland country.

For several years we have been trying to collect data on the fledging and incubation periods of local birds. To this end we have scrupulously avoided disturbing any nest found and we have endeavoured to get the history of each clutch. Especially in the forest our experience has led us to realise that the mortality of eggs and nestlings through the action of predators is enormous. In the forest, on the average, not one of our nests in a dozen has escaped destruction at some stage before the young are ready to fly. Often the nests themselves are torn to pieces. A heavy snake might break up a flimsy nest of twigs, but only an active quadruped could rend a closely woven nest like that of *Illadopsis stictigula* or *Trococercus albonotatus*. It appears that the squirrels, the flying squirrel and the *Cercopithecus* monkeys must be the chief mammalian enemies of birds in the tree-tops, and squirrels, Muridae and Viverridae in the lower strata.

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Local forest mammals that are unlikely to do any harm to birds are *Colobus palliatus* Ptrs., ranging all the forests and apparently a vegetarian; the elephant shrew, *Rhinionax p. petersi* Boc. and others of the Macroscelididae and Soricidae; the hyrax, *Procavia t. terricola* Mollison; and bats of several genera.

Some of the large owls and Falconidae depend mainly on rats and mice. Stomachs of *Lophaëtus occipitalis*, *Buteo* spp., and *Strix woodfordii* have contained them. A pair of ravens, *Corvultur albicollis*, have been seen hunting mice in a woodpile. The coucal, *Centropus superciliosus*, eats very small mice. Several of the larger carnivorous birds harry monkeys, but the only species actually seen eating one is the raven. There is evidence that the great eagle, *Stephanoaetus coronatus*, takes both monkeys and young antelopes.

Lower vertebrates.

The Usambara Mountains are rich in lower vertebrate life—there are for example nine different chameleons—in both species and numbers, but we know even less about their distribution in detail than we do about the mammals.

Frogs of all sizes swarm; and especially after a shower of rain the forest is filled with the castanet rattling of the tree frogs. Remains of frogs have been found in the stomachs of two coucals (*Centropus superciliosus* and *Ceuthmochares aereus australis*), but no other “land-bird” is known to eat them.

Both lizards and chameleons form an important part of the diet of some raptorial birds. In the Intermediate Zone they have been found in the stomachs of *Lophaëtus occipitalis*, *Buteo rufofuscus* *augur*, *Gymnogenys t. typicus*, *Circæëtus fasciolatus*, and also of a thrush, *Turdus olivaceus roehli*. In the Lowland Savannah lizards form the staple food of *Kaupifalco monogrammicus meridionalis*. There is no evidence that any of the lizards take birds' eggs or young, but the big monitor, *Varanus niloticus* (L.), is under suspicion.

Crocodiles, which abound in the rivers of the Lowland zone, the Pangani, Middle Sigi and Lwengera, do not live naturally in the Intermediate or Highland Zones. They were introduced into a mill-dam near Amani by an early settler, whose motives must remain profoundly obscure. Little grebe, moorhen and jacana (*Actophilus africanus*) besides three species of rail, manage to co-exist in the mill-dam with the crocodiles and to bring off their broods successfully.

The snake fauna certainly includes several species that take eggs or birds or both. The general impression gained personally and from Loveridge's work is that snakes in general are much less numerous in the Highland Zone than at lower altitudes.

Fish, which are plentiful and often large in the more slowly flowing waters of the Lowland Zone, diminish in both size and abundance at higher altitudes. In the Intermediate Zone fish up to about 9 in. long have been observed, though not commonly. In the Highland Zone waters (West Usambara) I am informed that there were no fish at all until trout were introduced a few years ago. As might be expected, the water-feeding birds diminish in numbers and

variety *pari passu* with the fish. None of the heron tribe occur above the Lowland Zone except as rare stragglers, and no kingfishers except *Alcedo semitorquata* and an occasional *Megaceryle maxima*. These also are absent from the Highland Zone, where the now abundant trout have failed to attract them.

INVERTEBRATES.

Insects.

A good deal of entomological collecting has evidently been done from time to time in our area, but published data on the insect fauna as a whole or on the distribution of individual groups are lacking. Dealing, as one is, with an insect fauna that is most imperfectly known, the specific identification of stomach contents presents even greater difficulties than usual. What little I have to say under this head is therefore only the generalised impression of a layman.

There appears to be a diminution in variety and abundance of insects in general with altitude. Mosquitoes, potentially of importance as vectors of bird malaria, of which nothing is at present known in Africa, are less numerous in the Intermediate than in the Lowland Zone and scarcer still in the Highland. Ants affect the economy of the local birds in three ways. They enter into the diet of many species, especially *Neocossyphus r. rufus* and *Alethe anomala montana*. As represented by the terrible *siafu*, which scour the country in irresistible columns, they are occasionally responsible for the death of nestlings. On the other hand in their foraging the *siafu* drive out of cover numbers of insects, e.g. small cockroaches, that normally lie up secure from birds in crevices and dense clumps of vegetation. The bunting, *Emberiza major orientalis*, a flycatcher, *Melaenornis tropicalis pammelaina*, and the drongo have been seen waiting upon an ant column in this way in the open.

Termites are greatly appreciated by birds. They are most abundant in the Lowland Zone, almost unknown in the Highlands, and not much in evidence inside the Evergreen Forests anywhere. Guinea-fowl will scratch at their workings to get at them, but unfortunately for the biological control of these insects they are only accessible to the attacks of the smaller birds when the nuptial swarms take wing from the termitaria. This takes place often on damp evenings. Then many different birds, including species not usually insectivorous, will gorge themselves on them. Orioles, drongos, starlings, geelgats and Falconidae have particularly been noted as taking flying termites until dark.

The grasshopper tribe (Orthoptera) is represented in great numbers both inside the Evergreen Forests and outside. They are taken according to their size by a wide variety of birds from grass-warblers to crows. For some, such as *Lanius fiscus humeralis*, they are a staple food. One local species, however, the "Stink Grasshopper," *Zonoceros elegans*, which is of some economic importance, appears to be avoided by practically all birds.

Locust swarms make occasional appearances in our area, more rarely in the mountains than in the surrounding plains. Full-grown locusts are, of course,

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beyond the capacity of most Passerine birds. In the dry country where they make their most frequent and destructive appearance their chief enemies are the raptorial birds, the storks, Phasianidae, Otidae, wattled starlings and rollers (*Coracias* spp.). In the mountains, besides raptorial birds, only the Corvidae (*Corvus albus* and *Corvultur albicollis*) and a kingfisher, *Halcyon albiventris orientalis*, have been noted as taking locusts. Probably many more birds eat them when they have settled on the forest canopy and are still torpid in the early morning. On the subject of birds and locust-hoppers in a neighbouring area of (Lowland) Thorn Country see Moreau (1930).

The status of the social Hymenoptera generally in the mountains is obscure. Direct indications of the abundance of bees, e.g. in the occurrence of native beehives and of the common honey-guide, *I. indicator*, are features of the Savannah of the Lowlands, but not of the upper zones. Bee-eaters (*Meropidae*) also are few and far between in the mountains. These facts might be taken to indicate a comparative scarcity of bees above the Lowland Zone, but such an impression may be incorrect. *Indicator variegatus* certainly flourishes in the plateau forests. One other member of the honey-guide family in the mountains, *Prodotiscus insignis ellenbecki*, relies upon a different order of wax-elaborating insects, the Coccidae.

Gasteropods.

The land Gasteropods are of some importance. They are common in the Evergreen Forests, where they bulk large in the food of a dove, *Aplopelia l. larvata*, the thrushes and the *Illadopsis* spp. The very large pale green slugs, up to four inches in length, have been observed to be taken by *Pitta angolensis longipennis* and *Centropus superciliosus* in captivity. Other observations on local birds in captivity make it appear possible that in these non-calcareous regions broken snail shells may be a source of lime for birds.

Other invertebrates.

In the forested districts of the mountains crabs are by no means confined to the streams. Especially in the rainy season they wander over the hills and even enter houses. They provide the favourite food of *Halycon albiventris orientalis* and have also been found in *Gypohierax angolensis* and *Gymnogenys t. typicus*. A feature of the Amani fauna that no one can fail to notice is the liver-coloured millipede about 6 in. long. In South Africa they are stated to be eaten by a hornbill, but there is as yet no evidence that any bird preys upon them in the Usambaras. Earthworms are not nearly so common as they are in English soil and they do not seem to be important in any of the birds' dietaries, although several species have been found in captivity to take them eagerly when they are offered.

PARASITES.

No particular attention has been paid to parasites on birds. Ectoparasites, especially *Mallophaga*, are often noticeable on the large birds, raptorial and ravens, on bank-martins (*Psaldoproctus*) and swifts. A striking exception to the general apparent freedom of the small birds from ectoparasites is afforded by *Bradypterus cinnamomeus*. Two of five shot in different parts of the West Usambaras in July 1931, each carried a large green Hippoboscid, not otherwise met with on the local birds. On one occasion a leech was found on the chin of a forest thrush (*Geokichla gurneyi usambarae*).

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THE PLANT COMMUNITIES OF TABLE MOUNTAIN

III. A SIX YEARS' STUDY OF REGENERATION AFTER BURNING

By R. S. ADAMSON.

(Department of Botany, University of Cape Town.)

(With Plate III.)

IN the preliminary account of the Plant Communities of Table Mountain (1), published in 1927, the prevalence of destruction by fire as a modifying influence on the vegetation was noticed. The present account records some features of the plant covering in a limited area in relation to regeneration after burning. The example chosen has been studied both before fire and afterwards for a period of six years. Owing to pressure of other occupations the study has been confined to observation. No detailed instrumental or other such work has been carried out on the changes brought about in the habitat.

The area selected is situated on the western slope of the mountain at an altitude of 800–900 ft. (244–274 m.) and has a uniform surface not complicated by drainage channels. The slope increases upwards from about 15° in the lower part to 20° above. The underlying rock is granite, but a considerable amount of sandstone debris overlies the rock. Exposures of the soil exhibit a layer 1–3 ft. (0.3–1 m.) in thickness composed of stones of varying size in a matrix containing a high percentage of sand. The reaction is neutral or very slightly acid (*pH* 6.75–7.0). The majority of the roots are confined to the sandstone detritus layer, though some do penetrate into the granite subsoil. The area is immediately below the highest point of the mountain ridge and is protected to a considerable extent from the prevalent south-easterly winds of the summer. Up to 1926 it was covered by fairly dense bush which was near the climax condition with definite layering. This community was figured in Part I of the present work (1, Pl. IX, phot. 4).

The upper layer, which was not continuous, was formed almost wholly of *Protea lepidocarpodendron*, the bushes reaching 1.5–1.75 m. in height. These bushes were generally distributed through the community, but only formed a continuous layer quite locally. They had an areal percentage of about 15. The only other plants occurring in this upper layer were very occasional bushes of *Protea grandiflora* and *Gymnosporia laurina*, both showing traces on their stems of past fires.

The second layer, which stood about 0.75–1 m. in height, was made up of a variety of shrubby plants in which the nanophyll and leptophyll nanophanerophytes predominated. The most abundant plants were *Metalasia muricata*,



Phot. 2. Details of the area in 1929. *Leucadendron plumosum* (l.c. and behind rock), *Euryops abrotanifolius* (r.c.), *Anthospermum aethiopicum* (front of rock), *Protea lepidocarpodendron* (large-leaved shoot, l.), *Pelargonium cucullatum* (pale flowers l.c.), *Stoebe cinerea* (r.c. foreground), also *Helichrysum auri-entatum*, *Picinia bracteata*, *Aspalanthus chenopoda*, and *Metelasia mimica*.



Phot. 1. General view of the community in October, 1928, 2 1/2 years after fire. Numerous plants of *Euryops abrotanifolius* forming an open vegetation.



Phot. 3. General view in 1931. *Euryops abrotanifolius* almost dominant. The larger bushes are *Leucadendron plumosum* and *Protea lepidocarpodendron*.



Phot. 4. General view in 1933. *Protea* now overtops the general bush level. *Metelasia*, *Euryops*, *Muraltia heisteria*, *Aspalanthus*

Leucadendron plumosum, *Stoebe aethiopica*, *St. cinerea*, *Erica plukenetii*, *E. baccans*, *Montinia acris* and *Royena glabra*. In all 92 species of flowering plants were recorded, a list of which is appended. In this condition the surface soil showed a loss of 5·8–7·3 per cent. on roasting.

The area was burnt in February 1927 by a fire that spread over a considerable area of the lower slopes on this side of the mountain. The fire, coming at the height of the dry season, destroyed the whole of the aerial parts of the plants. The first examination subsequent to the fire was made in October of that year, i.e. after an interval of eight months. At this time the ground was covered with dead charred stems of *Proteas* and other bushes, some still standing, but most fallen. The living plants present were all of small size, at a maximum 10–20 cm., and consisted of sprouts from still living shoots in the ground, geophytes, annuals, and a few invaders. The plant covering was very open and including all plants covered only about 10 per cent. of the soil surface. At this time 53 species in all were recorded for the area. A considerable number were geophytes or sprouts from the underground portions of bushes which had been burned back: *Royena glabra*, *Rhus lucida*, *Salvia africana*, *Osteospermum moniliferum* and *Pelargonium cucullatum* were the most prominent. *Restio cuspidatus* was also coming up from the rhizome. Of the geophytes, *Bobartia spathacea*, *Pelargonium triste*, with *Oxalis* spp. were the commonest. Annuals were present, but not in large numbers: *Sebaea exacoides*, *Usinia anthemoides* and *Manulea cheiranthus* were the commonest. Seedlings were fairly numerous, especially those of *Euryops abrotanifolius* and *Metalasia muricata*. *Protea lepidocarpodendron* seedlings were already appearing. In addition there were a few seedlings of *Aspalathus chenopoda*, *Hakea acicularis* and *Athanasia parviflora*, none of which were present before the fire. Besides these, other new plants found were *Albuca minor*, *Hibiscus aethiopicus*, *Lobostemon glaucophyllus* and *Wahlenbergia capensis*, together with weeds such as *Briza maxima* and *Homeria collina*, though none of them were at all abundant.

In 1928, eighteen months after the fire, the vegetation was still of an open character, but much more abundant and the plants provided a general cover. The general growth stood at about 1 ft. (30 cm.) in height, and about 40 per cent. of the area was covered. By far the most abundant plants were *Euryops abrotanifolius* and *Senecio pubigerus*, which now spread over the entire area. While very abundant, neither of these plants attained real dominance. *Euryops* grows from single erect shoots not much branched and *Senecio* is not a social plant. They do, however, provide a certain measure of protection, even if not controlling the growth of their neighbours by limitation either of light or of space. Other abundant species at this time were *Pelargonium cucullatum* which was flowering, *Muraltia heisteria*, *Osteospermum moniliferum* and *Anthospermum aethiopicum*. Prominent but less abundant plants were *Bobartia spathacea*, *Aspalathus chenopoda*, *Lobostemon fruticosus* and *Hermannia althaei-*

folia. Small plants and seedlings of *Leucadendron plumosum* were frequent and were coming up below the larger more prominent constituents, together with young plants of *Protea lepidocarpodendron* and *Metalsia muricata*. These were only 10–15 cm. high. The community at this stage was very varied, 84 species being noted. Numbers of plants occurred associated together without much distinction in abundance or differentiation into strata. Nine species present before burning, which had not been seen after the fire in 1927, were recorded, and 22 species were present which were not found in the original community. At this time much of the dead charred wood had disappeared, largely owing to the activities of collectors of firewood. The soil had become much more stony at the surface owing to the washing down of the finer material during the winter rains.

In 1929, after two and a half years, the number of species had risen to 105 and the vegetation was approaching the closed condition. The general level was 30–40 cm. in height. *Euryops abrotanifolius* was much the most abundant plant, but many others were appearing beneath or between its shoots. *Senecio pubigerus* had declined in abundance very considerably and at this time was only recorded as frequent. *Leucadendron plumosum* had become prominent, many of the plants equalling the *Euryops* in height and making with their pale leaves quite a prominent feature in the community. The young plants of *Protea* and *Metalsia* were still much lower in stature and sheltered beneath the taller bushes of *Euryops* and *Leucadendron*. The vegetation at this period was very mixed, numerous species occurring in association. Those that had sprouted from persistent basal parts were now crowded by invaders and less extensive in their spread. At this time 9 species recorded before the fire but not seen earlier in the subsera were noted, 11 species present in the earlier phases were not found and 26 additional species were present. Of these newcomers mention may be made of a number of low-growing plants, notably species of *Mesembrianthemum*, which had established themselves in the rather open conditions prevailing.

The next examination of the area was made two years later, in October 1931, after an interval of four and a half years from the fire. The vegetation by this time had changed somewhat, a quite continuous cover of the shoots forming the uppermost level of the community had been developed and reached a height of 60–70 cm. *Euryops abrotanifolius* was exceedingly abundant and gave an impression of complete dominance, which was especially marked at its flowering period, July–August. In fact, however, though the upper level was practically closed, this species occupied but a small proportion of the actual soil area and allowed the development of many others between. *Leucadendron plumosum* was especially abundant, and some bushes of this plant stood out above the general level of the *Euryops*. *Protea lepidocarpodendron* now attained a height equalling the general bush level and, though not at first sight conspicuous, actually formed an important constituent of

the community. Other bushes present in considerable numbers were *Muraltia heisteria*, *Aspalathus chenopoda*, *Royena glabra* and *Lobostemon fruticosus*. *Metalasia muricata*, which had not yet reached the flowering stage, was relatively inconspicuous though present in large numbers. Geophytes and annuals were distinctly less prominent than in the earlier more open phases.

This period, four and a half years after the fire, marked the climax in the social activity of *Euryops abrotanifolius*. In the following year, 1932, though still abundant, this species showed a decided diminution, both in actual numbers and in relative abundance. It no longer had the appearance of dominance but occurred scattered freely amongst other bushes of equal height and stronger lateral spread. At this period definite stratification in the bush layers was again becoming apparent. Many of the *Proteas* now clearly stood up above the general level of the community. This also occurred locally with *Hakea pectinata*, which had invaded one part of the area. The main layer was a very mixed one, the most prominent species being *Metalasia muricata*, *Muraltia heisteria*, *Aspalathus chenopoda* and *A. thymifolia*.

These general conditions of the community had become further emphasised in 1933, six and a half years after the fire. There was now a distinct approach to the original structure. *Protea lepidocarpodendron*, though much less abundant than before the fire, formed a distinct but far from complete upper layer. The bushes reached 1–1.5 m. and were flowering. The main shrub layer was much more mixed and irregular than in the original community. Small bushes and low-growing woody plants were mixed and alternated with the larger bushes. This was partly due to the presence of rather frequent dead bushes which had left gaps not yet closed up by larger plants. Among those that had died in this way were *Euryops abrotanifolius*, *Aspalathus chenopoda*, *Leucadendron plumosum*, *Anthospermum aethiopicum*, *Stoebe cinerea*, *Pelargonium cucullatum* and *Muraltia heisteria*, all of which had been prominent in the earlier phases.

The most abundant plants in the nanophanerophyte layer at this period were *Metalasia muricata*, *Leucadendron plumosum*, *Aspalathus thymifolia* and *Muraltia heisteria*. *Euryops abrotanifolius* was now not more than frequent. As compared with earlier phases the general growth was much denser with very few open patches of soil, but as compared with the original community the layering was distinctly less complete and the lower layer had a much greater number of small-leaved woody plants of xeromorphic habit. The percentage of these Chamaephytes, almost all undershrubs, had risen to 26 from 19 in the original community. The uppermost layer was rather less complete and was now composed of only one native species instead of three. Three aliens had appeared, and these, if capable of survival, will become part of the upper layer and, if they become abundant, will produce profound alterations in the community.

In 1933, 112 species were recorded as compared with 92 in 1926 before the fire. Of those in the original community 16 (17 per cent.), had apparently

not become re-established after six and a half years, but 63 (68 per cent. of the old, or 56 per cent. of the new flora) had done so. This number may seem small, but the general similarity of the two communities is evident. In these communities specific uniformity is often small owing to the phenomenon referred to in Part II of this work as "life-form dominance" and the ecological interchangeability of plants with identical life forms (2).

Throughout the period of observation 173 species have been noted in the area. Of the 92 originally present before the fire, 16 have not been seen subsequently and 81 new species have made their appearance. Of these new species 38 were temporary, occurring in the first three years but subsequently absent; 5 appeared only in 1927, 11 only in 1928, and 15 only in 1929. By 1933 14 additional species had made their appearance. Of the original flora 33 species were recorded at every examination.

When dealing with communities whose populations are as large as those in these stages of regeneration, and where specific dominance is lacking, comparisons are not very readily made without considerable elaboration and the inclusion of masses of detail; but some general features of the regeneration succession may be gathered from a consideration of the distributions of life forms in the different phases.

Throughout the series of stages that have been described, the differences are, in the main, due to differences in the relative abundance of the plants: the principal constituents remain constant throughout. The majority of the species invading after the fire are not very abundant, though exceptions occur, such as the species of *Aspalathus* and *Senecio pubigerus*, which become temporarily very abundant.

For purposes of simplification the whole series of stages through the six and a half years are not included in making the comparisons. The first three years, which represent the open phases, and the last will alone be dealt with, since these will sufficiently illustrate the salient features. For these periods the life-form spectra are as follows (the figures here and in the other tables being percentages to the nearest whole number):

	Total	M.	N.	Ch.	H.	G.	T.	E.
1926	92	2	37	19	19	19	4	—
1927	62	2	29	18	13	27	11	—
1928	84	1	29	20	15	23	10	—
1929	105	4	29	25	16	21	5	—
1933	112	4	36	26	15	15	3	1

From these figures the essential similarity between the re-established community of 1933 and the original one is apparent. The increase in the Chaemaphytes has already been commented on and is due, in part at any rate, to the present incomplete nature of the bush cover. The increase in the M. class in the later years is due to the invasion of aliens: *Hakea pectinata*, *Pinus pinaster* and *Acacia saligna*. Of these only the first is at all common and this only locally.

In the early stages of the regeneration succession there is a definite rise in the proportions of Geophytes and Therophytes, a rise which is temporary and not maintained. The rise in Geophytes especially is not only proportional but an actual increase; in 1926 there were 17, in 1928 20, and in 1929 22.

The percentage of annuals is never large. Indeed, considering the quite open nature of the vegetation in the early phases the numbers are unexpectedly low. This is correlated with the soil and habitat conditions: annuals are much more abundant on sands and on the sheltered slopes. The winters of 1927 and 1928 were both characterised by rainfall below the average, and this is possibly a contributory factor to the small numbers of Therophytes.

Throughout the series the percentages of the N. and H. classes show little variation. A further analysis, however, brings out some features of interest:

	Nanophanerophytes			
	Microphylls	Nanophylls	Leptophylls	With compound leaves
1926	1	12	20	3
1927	2	13	8	6
1928	1	14	12	2
1929	1	11	15	2
1933	2	12	19	2

From these figures it appears that immediately after fire there is an alteration in the proportions of nanophylls and leptophylls, the former becoming the more abundant. This is correlated with the behaviour of the plants; a large number of the nanophylls regenerate from the base, whereas this characteristic is not shown by any of the leptophylls, which only reproduce from seed and in some cases not immediately. Slowness of regeneration is a marked feature of some of the leptophylls, for example members of the Ericaceae. Not one of these was found in the first three examinations after the fire, and even in 1933 two which occurred originally had not reappeared—*Erica petiveri* and *Blaeria ericoides*.

This lag in the re-establishment of leptophylls is not very markedly shown in the figures, except in those for 1927, because it is masked by the rapid growth of plants of short duration, of which *Aspalathus chenopoda* is a characteristic example. In the open phases these plants enter and by rapid growth attain a considerable importance in the community, only to be later displaced altogether or reduced to an inconspicuous rôle. *Senecio pubigerus* and *Euryops abrotanifolius*, though not leptophylls, behave in the same way.

While the total percentage of Hemicytrophytes shows a small diminution, the different subclasses exhibit differences which seem to be significant.

	Hemicytrophytes		
	With assimilating stems	Grass-like plants	Others
1926	3	8	8
1927	3	5	5
1928	2	11	2
1929	2	10	4
1933	3	10	3

The subdivisions in the above table are those used in a previous paper (2). The division headed "others" in this vegetation consists almost entirely of rosette-like plants without elongated stems. The rhizomatous herb is here very unusual.

Plants with assimilating stems or with erect stem-like leaves show little variation in numbers. The plants most abundant in this class are the Restionaceae, which are never abundant on soils derived from granite, either as constituents of the community or in variety of species. They become of much more importance on the sandy soils.

Grass-like plants show a small increase, which commences in the second year and persists. The increase of these plants in the community is larger than the figures suggest: the species have increased both in number and in areal percentage. The last was unfortunately not measured in 1926, but in 1929 was 3.75, and in 1933 3.25. Originally it was certainly less than this. The increase is both in true grasses and in Cyperaceous plants. None of them is individually abundant.

The remaining Hemicytrophytes show a decrease that is even more marked than appears from the figures. Before the fire this class was represented principally by plants with relatively broad leaves, e.g. *Knoultonia hirsuta*, *Lichtensteinia lacera*, *Arctotis acaulis*, etc., or by definite shade-loving plants such as *Cineraria geifolia*. These have largely disappeared: *Arctotis* has persisted and *Lichtensteinia* reappeared in 1932; but the others, five in number, have not been seen since the fire. In the regeneration stages this class is represented by plants with smaller leaves, favouring more exposed conditions, e.g. *Hydrocotyle solandra*. The loss of these broader-leaved and shelter-loving Hemicytrophytes, the increase in grass-like plants and in Chamaephytes, produces in the present community a more xeromorphic general facies than was the case in the original one. Observations continued over a longer period are needed before the possibility or otherwise of complete regeneration can be made out.

The original community here had itself been burned in the past and it is probable that the alterations seen in the six years of the last regeneration are changes of a kind that have become more pronounced with successive fires. The simplification of the upper layers, the general increase in xeromorphism, and the increasing proportions of smaller woody plants and elimination of the larger-leaved and shade-loving species are cumulative. With the prevalence of fires, which has continued for so long, it is now practically impossible to find a community in which these changes have not been initiated.

While fire is of such extremely common occurrence in the sclerophyll vegetation of the Cape region, very little work has so far been done in studying the real effects produced on the plant communities. Compton (5), Phillips (10), and others (4, 7, 11) have dealt with the subject in general terms. Detailed work has been confined to the first stages of regrowth. Michell (Levy's) (9)

described the growth immediately following fire on Signal Hill. In this investigation the soil conditions were not the same as those in the example here described, and the original community was a simpler one of less advanced type. After the fire there was a marked increase in Geophytes, but not a large increase in annuals. Later *Senecio pubigerus* showed a considerable increase in importance, though less than in the present case. On Signal Hill *Elytropappus rhinocerotis* appeared to be about to assume dominance on the burnt area. This dominance of *Elytropappus* was demonstrated by the later and more detailed work carried out by Levyns at Stellenbosch (8). Here again the first phases are characterised by numbers of Geophytes and rather few annuals. This paucity of annuals is also seen in the phases of regeneration after fire in the Stringybark forests in South Australia (3), but is in striking contrast with the conditions after fire in the sclerophyll vegetation of California, where Cooper (6) records 22 annuals out of 28 recognisable species in the first season. In the sclerophyll vegetation of Europe Geophytes become very prominent following a fire, and are associated with annuals. There, however, the numbers of species in each class is much smaller than in South Africa. In the macchia of Corsica, for example, *Asphodelus microcarpus* becomes exceedingly abundant after fire and may form almost pure communities (12).

The temporary assumption of dominance by one or more species which ordinarily are absent from, or of slight importance in, the stable vegetation is a general phenomenon, at any rate among sclerophyll communities, and can be seen in many other types. At the Cape, besides *Euryops abrotanifolius*, such plants as *Elytropappus rhinocerotis*, *Aspalathus chenopoda*, and others, occupy this rôle. In South Australia (3) *Ixodia achillaeoides* assumes temporary dominance under the trees, in Corsica (12) *Cistus monspeliensis*, and in California (6) *Ceanothus cuneatus*, behave in this manner.

The degree of dominance and the length of time during which these species persist vary very considerably. In the present case *Euryops* assumed the predominant rôle after two and a half years and persisted for two to three years, afterwards being rapidly reduced by the competition of other more permanent species. *Elytropappus*, on the other hand, is a much more persistent species and the same is true of *Cistus monspeliensis* in Corsica.

The longer such plants retain their importance the more extended is the alteration produced by the fire.

SUMMARY.

1. The regeneration of a climax community after destruction has been traced through a period of six years.
2. At the end of this period the vegetation had returned to a condition similar to, but not identical with, the original.

3. In the early stages the shrubs regenerated partly from shoots and partly from seed.

4. Temporary dominance was assumed by *Euryops abrotanifolius* after three years. After five years the plant was rapidly reduced in quantity.

5. The number of species showed a progressive increase, being larger than the original number at the end of the period.

6. The salient features of the community at yearly intervals are described.

7. The relations of the prevalent life forms are dealt with. In the early stages there was a distinct increase in Geophytes and a small one in annuals. Chamaephytes showed a progressive increase.

8. Immediately after the fire there was an increase in the ratio of nanophyllous to leptophyllous Nanophanerophytes owing to the fact that many of the former sprout freely from the base after burning while the latter regenerate only from seed. Grass-like Hemicryptophytes increased and relatively broad-leaved Hemicryptophytes decreased in percentage after burning, giving a more xeromorphic facies to the vegetation.

9. General comparisons are made with other sclerophyll types. Those of the southern hemisphere are poor in annuals as compared with northern examples. All show the initial increase in Geophytes and temporary large increase of one or more shrubby plants.

LIST OF SPECIES.

The following abbreviations for the names of life forms are employed: M. mic. = Microphanerophyta microphylla. M. cpd. = Microphanerophyta with compound leaves. N. nano. = Nanophanerophyta nanophylla. N. lept. = Nanophanerophyta leptophylla. N. cpd. = Nanophanerophyta with compound leaves. Ch. nano., Ch. lept., Ch. cpd. = Chamaephyta with the corresponding leaf forms. H. as. st. = Hemicryptophyta with assimilating stems. H. gr. = Grass-like Hemicryptophytes.

	Life form	1926	1927	1928	1929	1933
<i>Acacia saligna</i>	M. mic.	—	—	—	x	x
<i>Adenandra uniflora</i>	N. nano.	—	—	x	x	x
<i>Agathosma imbricata</i>	N. lept.	x	x	x	x	x
<i>A. multicaulis</i>	N. lept.	—	—	—	—	x
<i>Agathelpis angustifolia</i>	Ch. lept.	—	—	—	x	x
<i>Anapalina revoluta</i>	G.	x	x	x	x	x
<i>Anthospermum aethiopicum</i>	N. lept.	x	x	x	x	x
<i>Albucca minor</i>	G.	—	x	x	x	x
<i>Arctotis acaulis</i>	H.	x	x	x	x	x
<i>Aristea cyanea</i>	G.	x	—	—	x	x
<i>Aristida capensis</i>	H. gr.	—	—	—	—	x
<i>Aspalathus chenopoda</i>	N. lept.	—	x	x	x	x
<i>A. thymifolia</i>	N. lept.	—	—	x	x	x
<i>A. ? canescens</i>	Ch. lept.	—	—	—	—	x
<i>Asparagus thunbergianus</i>	G.	x	—	x	—	—
<i>Aster fruticosus</i>	Ch. lept.	—	—	—	—	x
<i>Athanasia parviflora</i>	N. cpd.	—	x	—	—	—
<i>Babiana disticha</i>	G.	x	x	x	x	x
<i>Baeometra columellaris</i>	G.	—	—	x	x	—
<i>Berkheya rigida</i>	H.	x	—	—	—	—
<i>Blaeria ericoides</i>	N. lept.	x	—	—	—	—
<i>Bobartia gladiata</i>	G.	x	x	—	—	x
<i>B. spathacea</i>	G.	x	x	x	x	x
<i>Borbonia cordata</i>	N. nano.	x	x	x	x	x
<i>Briza maxima</i>	T.	x	x	—	—	x

	Life form	1926	1927	1928	1929	1933
<i>Brizopyrum capense</i>	H. gr.	x	—	x	x	x
<i>Cassytha ciliolata</i>	E.	—	—	—	—	x
<i>Cenia turbinata</i>	T.	—	—	x	—	—
<i>Cerastium capense</i>	T.	—	x	—	—	—
<i>Chrysocoma coma-aurea</i>	N. lept.	x	—	—	x	x
<i>Cineraria goifolia</i>	H.	x	—	—	—	—
<i>Cliffortia juniperina</i>	N. lept.	x	—	—	x	x
<i>C. polygonifolia</i>	N. nano.	—	—	x	x	x
<i>C. ruscifolia</i>	N. nano.	x	x	x	x	x
<i>Danthonia macrantha</i>	H. gr.	x	—	—	x	x
<i>Diascia</i> sp.	T.	x	—	x	—	—
<i>Diosma vulgaris</i>	N. lept.	x	—	—	—	—
<i>Disa micrantha</i>	G.	—	—	—	—	x
<i>Dischisma ciliatum</i>	T.	—	—	x	—	—
<i>Disperis capensis</i>	G.	x	—	—	—	—
<i>Dorotheanthus criniflorus</i>	T.	—	—	x	—	—
<i>Ehrharta calycina</i>	H. gr.	x	—	x	x	x
<i>Elegia juncea</i>	H. as. st.	—	—	—	—	x
<i>Elytropappus rhinocerotis</i>	N. lept.	x	—	—	x	—
<i>Erica baccans</i>	N. lept.	x	—	—	—	x
<i>E. petiveri</i>	N. lept.	x	—	—	—	—
<i>E. pluckenetii</i>	N. lept.	x	—	—	—	x
<i>E. pusilla</i>	N. lept.	x	—	—	—	x
<i>Eriocephalus umbellulatus</i>	N. lept.	—	—	—	x	—
<i>Eriospermum cernuum</i>	G.	x	—	—	—	—
<i>E. lanceolatum</i>	G.	—	—	—	x	x
<i>Euphorbia lanceolata</i>	G.	—	—	—	x	x
<i>Euryops abrotanifolius</i>	N. epd.	x	x	x	x	x
<i>Ferraria undulata</i>	G.	—	x	—	—	—
<i>Festuca rigida</i>	H. gr.	—	—	x	—	—
<i>Ficinia bracteata</i>	H. gr.	—	—	—	x	x
<i>F. filiformis</i>	H. gr.	x	x	x	x	x
<i>F. setiformis</i>	H. gr.	x	x	x	x	x
<i>F. tribracteata</i>	H. gr.	—	—	x	x	x
<i>Geissorrhiza secunda</i>	G.	—	—	x	—	—
<i>Gnaphalium candidissimum</i>	T.	—	—	x	—	—
<i>Gymnosporia laurina</i>	N. nano.	x	—	—	—	—
<i>Haemanthus coccineus</i>	G.	x	x	—	—	x
<i>Hakea acicularis</i>	N. lept.	—	x	x	x	x
<i>H. pectinata</i>	M. cpd.	—	—	—	x	x
<i>Helichrysum auriculatum</i>	Ch. nano.	x	—	—	—	x
<i>H. cymosum</i>	Ch. lept.	x	x	x	x	x
<i>H. teretifolium</i>	Ch. lept.	x	—	x	x	x
<i>Helichrysum</i> sp.	Ch. nano.	—	—	x	x	x
<i>Heliophila scoparia</i>	Ch. nano.	—	—	x	x	x
<i>Heliophila</i> sp.	T.	—	—	—	x	—
<i>Helipterum gnaphaloides</i>	Ch. nano.	—	—	—	—	x
<i>Hemimeris montana</i>	T.	—	—	x	—	—
<i>Hermannia althaeifolia</i>	Ch. nano.	x	—	x	x	x
<i>H. cuneifolia</i>	Ch. nano.	x	x	x	x	x
<i>H. vesicaria</i>	Ch. nano.	—	—	—	x	x
<i>Hesperantha radiata</i>	G.	—	—	x	—	—
<i>Hibiscus aethiopicus</i>	Ch. nano.	—	x	x	x	x
<i>Hippia gracilis</i>	H.	—	—	—	x	—
<i>Homeria collina</i>	G.	—	x	x	x	—
<i>Hydrocotyle solandra</i>	H.	—	x	x	x	x
<i>H. virgata</i>	Ch. lept.	x	—	—	—	x
<i>Iffoga laricina</i>	Ch. lept.	—	—	—	x	x
<i>Indigofera coriacea</i>	Ch. cpd.	—	x	x	x	x
<i>Knowltonia hirsuta</i>	H.	x	—	—	—	—
<i>Lachenalia orchoides</i>	G.	x	x	x	x	—
<i>Lasiochloa ciliaris</i>	H. gr.	—	—	—	x	x
<i>Lessertia pulchra</i>	H.	x	—	—	—	—
<i>Leucadendron adscendens</i>	Ch. nano.	x	—	x	x	x
<i>L. plumosum</i>	N. nano.	x	—	x	x	x
<i>Lichtensteinia lacera</i>	H.	x	—	—	—	x
<i>Lobelia pinifolia</i>	Ch. lept.	x	—	—	—	—

	Life form	1926	1927	1928	1929	1933
<i>Lobostemon fruticosus</i>	N. nano.	x	x	x	x	x
<i>L. glaucophyllus</i>	N. nano.	—	x	x	x	x
<i>Lotononis</i> sp.	H.	—	—	—	x	—
<i>Manulea cheiranthus</i>	T.	—	x	x	—	x
<i>Mesembrianthemum</i> sp. (1)	Ch. nano.	x	x	x	x	x
<i>Mesembrianthemum</i> sp. (2)	Ch. nano.	—	—	—	x	—
<i>Mesembrianthemum</i> sp. (3)	Ch. nano.	—	—	—	x	—
<i>Mesembrianthemum</i> sp. (4)	Ch. nano.	—	—	—	x	—
<i>Metalsasia cephalotes</i>	N. lept.	x	—	—	—	—
<i>M. divergens</i>	Ch. lept.	—	—	—	x	x
<i>M. muricata</i>	N. lept.	x	x	x	x	x
<i>Moraea tripetala</i>	G.	—	—	x	x	x
<i>Moraea</i> sp. (yellow)	G.	—	x	x	x	x
<i>Moraea</i> sp.	G.	—	—	x	x	—
<i>Muraltia heisteria</i>	N. lept.	x	—	x	x	x
<i>Myrsine africana</i>	N. nano.	—	—	x	—	—
<i>Montinia acris</i>	N. nano.	x	—	—	—	x
<i>Oftia africana</i>	Ch. nano.	—	—	—	—	x
<i>Ornithogalum</i> sp.	G.	—	—	x	—	—
<i>Osteospermum ciliatum</i>	Ch. nano.	x	x	x	x	x
<i>O. moniliferum</i>	N. nano.	x	x	x	x	x
<i>Oxalis bifida</i>	G.	x	—	—	x	—
<i>O. cernua</i>	G.	—	—	—	x	—
<i>O. obtusa</i>	G.	x	x	x	x	x
<i>O. polyphylla</i>	G.	—	x	—	x	—
<i>O. variabilis</i>	G.	x	x	x	x	x
<i>O. versicolor</i>	G.	—	—	—	x	—
<i>Passerina filiformis</i>	N. lept.	—	—	—	—	x
<i>P. vulgaris</i>	N. lept.	x	—	x	x	x
<i>Pelargonium cucullatum</i>	N. mic.	x	x	x	x	x
<i>P. myrrhifolium</i>	Ch. cpd.	x	x	x	x	x
<i>P. tabulare</i>	Ch. nano.	x	x	x	x	x
<i>P. triste</i>	G.	x	x	x	x	x
<i>Pentaschistis aspera</i>	H. gr.	—	—	x	x	x
<i>P. curvifolia</i>	H. gr.	x	—	—	x	—
<i>P. thunbergii</i>	H. gr.	x	x	x	x	x
<i>Peucedanum galbanum</i>	N. cpd.	x	—	—	—	—
<i>Pharnaceum lanatum</i>	Ch. lept.	—	x	x	—	—
<i>Phylica stipularis</i>	N. lept.	—	—	x	x	x
<i>Pinus pinaster</i>	M. mic.	x	—	—	x	x
<i>Podalyria sericea</i>	N. nano.	x	—	x	x	x
<i>Priestleya villosa</i>	N. nano.	x	x	—	x	x
<i>Protea acaulis</i>	Ch. mic.	x	—	—	—	—
<i>P. grandiflora</i>	M. nano.	x	x	x	x	x
<i>P. lepidocarpodendron</i>	M. mic.	x	—	—	—	—
<i>Pterygodium catholicum</i>	G.	—	—	—	x	—
<i>Rafnia affinis</i>	Ch. lept.	x	x	x	x	x
<i>Restio cuspidatus</i>	H. as. st.	x	x	x	x	x
<i>R. gaudichaudianus</i>	H. as. st.	x	—	—	—	x
<i>Restio</i> sp.	H. as. st.	x	x	—	—	—
<i>Rhus lucida</i>	N. cpd.	x	x	x	x	x
<i>R. stenophylla</i>	Ch. cpd.	—	—	—	—	x
<i>R. tomentosa</i>	N. cpd.	—	x	—	—	—
<i>Rochea odoratissima</i>	Ch. nano.	x	—	—	—	x
<i>Roella ciliata</i>	Ch. lept.	—	—	—	x	—
<i>Royena glabra</i>	N. nano.	x	x	x	x	x
<i>Rumex cordatus</i>	G.	x	x	x	—	—
<i>Salvia africana</i>	N. nano.	x	x	x	x	x
<i>Sebaea aurea</i>	T.	—	—	—	x	—
<i>S. exacoides</i>	T.	x	x	x	x	x
<i>Selago spuria</i>	Ch. lept.	x	x	x	x	x
<i>Senecio burchellii</i>	Ch. lept.	x	—	—	x	—
<i>S. elegans</i>	T.	—	—	—	—	x
<i>S. grandiflorus</i>	H.	x	x	—	—	—
<i>S. pubigerus</i>	Ch. nano.	—	x	x	x	x
<i>Sporobolus indicus</i>	H. gr.	—	—	x	—	—
<i>Stoebe aethiopica</i>	N. lept.	x	—	—	—	x

	Life form	1926	1927	1928	1929	1933
Stoebe cinerea	N. lept.	x	—	—	x	x
Stoebe sp. (cf. cinerea)	N. lept.	—	—	—	x	—
Struthiola erecta	N. lept.	—	—	—	—	x
S. longiflora	N. lept.	—	—	—	—	x
Tetralia ustulata	H. as. st.	—	—	x	x	x
Themeda triandra	H. gr.	x	—	—	—	—
Thesium strictum	N. lept.	x	—	x	x	x
Thesium sp.	Ch. lept.	—	—	—	x	x
Ursinia anthemoides	T.	—	x	x	x	—
U. dentata	Ch. cpd.	x	—	—	—	x
Wachendorfia paniculata	G.	x	—	—	—	x
Wahlenbergia capensis	T.	—	x	—	—	—
Watsonia rosea	G.	x	x	x	x	x
Zalusianskya sp.	T.	—	—	x	—	—

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THE TRANSITION FROM WOODLAND AND MOORLAND TO GRASSLAND IN THE SPEY VALLEY AND ELSEWHERE

By E. WYLLIE FENTON.

INTRODUCTION.

RECORDS of the changes in the vegetation which occur when woodland or moorland is replaced by grassland are generally lacking. Yet the result of this process with the general breaking in of land for agriculture has completely transformed the vegetation and, in consequence, the appearance of vast areas of Britain. There are some places where the process may be seen at work, and these examples to some extent recapitulate one of the methods used in the very early days of agriculture in Britain. Within recent times, in certain parts of Scotland, one method usual in breaking in woodland and rough land to agriculture was first to stock with cattle. This increased grass and broke down and destroyed much of the taller vegetation. The remaining scrub and trees were then removed, and if the result was considered satisfactory, the land was finally broken up by the plough. Sometimes the area was left as permanent grassland.

The writer has seen several examples of the transition from woodland and moorland to grassland, and in 1933 a visit to that part of the Spey Valley from the Aviemore district to Grantown-on-Spey (average elevation 700 ft.) supplied much interesting information concerning the stages of transition. The survey was undertaken primarily to investigate the relationship of Juniper to woodland and also to grassland. It was found, however, that this necessitated a survey of the whole transition from woodland to grassland. The present article is the result of this investigation with some information collected from other districts.

The geological aspect of the Spey Valley has been described by Geikie (4). The River Spey has been dealt with by Hinxman (7), while Dr Newbigin's admirable study (10) of the Kingussie district (next to Aviemore) renders any further discussion on the geographical side unnecessary.

WOODLANDS.

The woodlands such as now survive in the Spey Valley are chiefly Scots Pine (*Pinus silvestris*). Much of the area was, or had been, semi-natural and some natural. There are also planted areas which were not investigated. During the period 1914-18 much of the woodland was cut, and for the most part there has been no extensive planting to replace the heavy losses. In some parts natural regeneration of Scots Pine may be found, but Birch (*Betula alba*) is making much more rapid progress. Oak occurs in small scattered areas—chiefly *Quercus sessiliflora*, but *Q. robur* was also found. In

one or two places trees have arisen from stooled oaks cut many years ago. In this respect they resemble many of the oaks found growing on Craigen-darroch, Ballater, Aberdeenshire: a fact recorded by Macgillivray in 1855 (9). In one instance Oak and Pine overlapped. R. Smith (11) remarks on coppiced Oak in North Perthshire, stating that it was a feature of the Highland Border but practically ceased at Blair Atholl.

The tree which has been, and still is, dominant is Scots Pine. Some of the woods are of considerable age, and in the older more open woods Juniper (*Juniperus communis*) is a common associate of Pine. The ground flora is generally dominated by Heather (*Calluna vulgaris*) if the wood is fairly open, and in the other cases by Blaeberry (*Vaccinium Myrtillus*). In some parts Birch has invaded the woods and now competes with Juniper. When Birch has been successful and is spreading, Juniper is seriously affected and tends slowly but surely to disappear. The chief reason is that Juniper is very intolerant of shade. If the Juniper trees—for not infrequently in open woods they reach a tree-like growth—are well established, they may hold their own with Birch. Under these conditions, however, it is very difficult for Juniper seedlings to grow to any height or to compete with the faster growing Birch. Where fires have occurred the Juniper is almost invariably killed unless it occupies a position where the flames cannot reach it. Birch, though often killed, may survive, especially if it has reached a more mature growth. After such fires Heather is often temporarily replaced by Blaeberry, which follows an ephemeral phase of Wavy Hair Grass (*Deschampsia flexuosa*).

After the cutting and clearing of Pine trees, Juniper remains for a long period. This was seen both in old woodland areas, moors, and grasslands as well as on hillsides where sheep were grazing. In several enclosed fields Juniper still remained as closely cropped small bushes surrounded by a Bent-Fescue grassland. An examination of a few fields showed that these enclosed fields or grasslands with the Juniper bushes scattered through them had never been under the plough. After the cutting and removal of the Pine trees, animals had been turned on to graze and as a result a Bent-Fescue grassland had developed. Some of these fields had a light covering of soil resting on peat, while 1½–2 ft. below the surface Pine and Birch remains (Upper Forestian Period (8)) were visible where a drainage ditch had been cut at the side of a field. Juniper may also be found when the Oak and not the Pine is the dominant tree.

The writer is indebted to Prof. K. W. Braid for conducting him over part of the Trossachs where the vegetation shows marked differences from the Spey Valley. Around Aberfoyle and Loch Katrine the vegetation is essentially open Oak wood with Birch and Juniper occurring in several places but seemingly never plentiful or widespread. Scots Pine is found only occasionally, either as a small community or scattered individually. The ground vegetation is frequently Heather, occasionally Bell Heather (*Erica cinerea*) with smaller

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patches of Cross-leaved Heath (*Erica Tetralix*) and occasionally stretches or patches of heathy grassland. Bracken is plentiful over considerable tracts.

Much of the agricultural land in the Trossachs and Aberfoyle area is obviously derived from the vegetation described above. The changes in the few grassland or grazed areas examined seemed to follow generally the changes noted in the Spey Valley district: that is, to Heather and Bent-Fescue types unless broken up and resown. No detailed study of the grasslands were made but there were resemblances to the grassland derived from degenerate oakwood (1).

A glance at the Vegetation Map of Scotland by Hardy (6) shows that the Spey Valley is essentially a Pine area with isolated small patches of Oak, but the Trossachs is an Oak area with small patches of Pine. Perhaps the best explanation of such conditions is afforded by Robert Smith (11) in dealing with the region of deciduous trees in North Perthshire:

"We can readily conceive that before human influence restricted the range of the different species a keen competition existed between the Oak and the Scots Pine for possession of the area. The general climatic conditions of the land below 1000 feet are suitable for either species. If the two species start equally well and in close proximity, the Oak tends to crush out the Pine, both by reason of its deeper shade and of its stronger branches. Where a clearing has been made, however, or where water has accumulated from ill-drainage and moss has sprung up and formed peat, or where animals graze on the seedlings, the Pines tend to spring up more readily and may for a time restrain the spreading of the Oak. The remains of both species are found in the peat bogs and probably each alternatively dominated over the land."

The conditions outlined above may explain the present vegetation of the Trossachs. It would also suggest that the patches of Juniper met with either on the top of rounded knolls or again in hollows are the sole survivors of what were once patches of open Pine wood. The Pines have long since disappeared, but the Junipers still stubbornly hold their ground.

Robert Smith (12) in discussing the region of deciduous trees in the Edinburgh district states: "The last patches of deciduous woodland coincide approximately with the last cultivated fields and often serve to shelter them from the wind." As the writer has shown elsewhere (1, 3) some of the grasslands of Devonshire are virtually degenerate Oak woodlands. The Neutral Grassland Association of ecologists (see *Types of British Vegetation*, edited by Tansley) gives added support to this statement. Much, if not most, of the arable land of Britain to-day has in all probability once been woodland.

MOORLAND.

In the Aviemore district there are extensive moors which may be put into two categories—those on light sandy gravel and those on peat. Apart from such situations as hillsides, valleys and declivities, peat is seldom deep. Where the peat had wasted from the edge, except in a few areas, particularly between

Aviemore and Inverness, the depth was seldom more than 2 ft., at which depth gravel or mineral soil or rock was met with.

For the most part Heather was the dominant plant. Bearberry (*Arctostaphylos uva-ursi*) was very plentiful on the sandy and gravelly moors and became locally dominant, spreading rapidly over any surface left bare after burning, or by human interference. It is very intolerant of shade and disappeared if any taller growing vegetation overshadowed it. Where Heather was burned, after a rapid transitional dominance by Wavy Hair Grass (*Desch. flexuosa*), Blaeberry tended to gain temporary dominance, though in some places it was replaced by Bell Heather (*Erica cinerea*). Generally in course of time Heather regained the dominant position. Many of these moors, however, are so frequently burned and the vegetation so constantly upset that they are quite unreliable indicators of the normal plant succession. There are a few, however, which have not been interfered with by man for a long time. These are interesting and give some indication of the origin of such moors. Frequently Scots Pine will be found in small clumps or patches, sometimes merely a few solitary trees. Sometimes the trees are old and occasionally there seemed to be a slow natural regeneration. Sometimes stumps of old Pine trees could be found. Birch was not infrequent and was often spreading over parts of the moor. Junipers also occurred, often in small clumps, but never plentifully. Where sheep were grazing these wide spaces, occasional patches of Bent-Fescue grassland occurred, while rabbits when present assisted the same association to maintain itself. Several other grasses were usually evident where there was grazing. The most noticeable feature, however, was the comparative scarcity of Moor Mat Grass (*Nardus stricta*), doubtless due to the fact that the grazing was not intensive.

Some of these moorlands have once been woodland, some a mixture of moorland and rather open woodland with scrub, and others have probably never been other than moorland. In some there are quite obvious traces of both wood and scrub growth, but these phases have long since ceased to exist. Intentional as well as possibly accidental burning has, in certain areas, been largely responsible for the present dominance of moorland, although on the fringes Birch is tending to gain a footing. Much of the moorland suggests considerable resemblance to what occurs both in Germany and in other parts of Scotland as pointed out by W. G. Smith (13).

GRASSLANDS.

The grasslands examined were with few exceptions semi-natural grasslands (14). Many of them had never been under the plough and only occasionally were they fenced into the size of ordinary pasture fields. Fences often are merely to keep stock from straying too far, or off roads or railway lines or from crossing a stream into other territory. In such areas the stocking is too light to enable the farmer or shepherd to exercise any control over the

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grazing. In many parts so light and scattered is the grazing that it can scarcely be called selective.

Grasslands derived from woods. A field derived from an old Pine wood consisted at the time of examination of the following: Wavy Hair Grass (*Deschampsia flexuosa*) and Bent Grasses (*Agrostis canina* + *vulgaris*)—dominant; Sheep's Fescue (*Festuca ovina*, including Red Fescue, *F. rubra*), Tormentil (*Potentilla erecta*) and Mosses—sub-dominant; with Heather, Bell Heather, Blaeberry, Field Wood Rush (*Luzula campestris*), Heath Rush (*Juncus squarrosus*), Moor Mat Grass (*Nardus*) (local) and a few plants of Dwarf Whin (*Genista anglica*) and Yorkshire Fog Grass (*Holcus lanatus*). The wood adjoining this field and still left intact contained Scots Pine and Juniper with a ground vegetation of Heather, Wavy Hair Grass, Cow Wheat (*Melampyrum pratense* var. *montanum*), Tormentil, Blaeberry and Bearberry, Sheep's Fescue, and a little Bent Grass.

Another field which had for a longer time been subjected to grazing showed much the same flora, but Bent Grasses were dominant, Sweet Vernal Grass (*Anthoxanthum odoratum*) was plentiful, while Devil's Bit Scabious (*Scabiosa succisa*), Scottish Bluebell or Hairbell (*Campanula rotundifolia*), Mountain Everlasting (*Antennaria dioica*) and Field Gentian (*Gentiana campestris*) were also present.

A field close to those just described had originally been seeded down but had been very badly treated. The flora consisted of Bent Grasses dominant; and Sheep's Fescue, Yorkshire Fog, Creeping Soft Grass (*Holcus mollis*), Eyebright (*Euphrasia officinalis*), Sweet Vernal Grass, Wavy Hair Grass; while less plentiful were Ribwort Plantain (*Plantago lanceolata*), Yellow Rattle (*Rhinanthus Crista-galli*), Dog's Tooth Lichen (*Peltigera canina*), Mosses, Self Heal (*Prunella vulgaris*), Ragwort (*Senecio Jacobaea*), Heather, Red Clover (*Trifolium pratense*), Wild White Clover (*T. repens*), Alsike Clover (*T. hybridum*) and Bird's Foot Trefoil (*Lotus corniculatus*).

A pasture typical of many sown down and near those derived direct from old woodland gave the following flora: Bent Grasses dominant, Sweet Vernal Grass sub-dominant; also present, Crested Dogstail Grass (*Cynosurus cristatus*), Cocksfoot Grass (*Dactylis glomerata*), Sheep's Fescue, Rat's Tail Fescue Grass (*Festuca Myuros*), Yorkshire Fog, Sheep's Sorrel (*Rumex Acetosella*), Wild White Clover, Red Clover and Alsike Clover, Bird's Foot Trefoil, Self Heal, Mouse-ear Chickweed (*Cerastium triviale*), Ragwort, Eyebright, Yellow Rattle, Hawkweeds (*Hieracium*) and Cudweed (*Gnaphalium sylvaticum*).

Many of the pastures which had been sown down had Bent Grass dominant and Sweet Vernal Grass sub-dominant on the lighter soils, and Bent Grass and Yorkshire Fog sub-dominant on the heavier and more acid soils. Even when Yorkshire Fog Grass was sub-dominant Sweet Vernal Grass was often plentiful. All natural or semi-natural grasslands, either large or small areas consisted essentially of Bent Grasses (*Agrostis canina* + *A. palustris* Huds.)

and Sheep's Fescue. In some Bent Grass was dominant, in others Sheep's Fescue.

Two examples from Berwickshire will suffice to show that the changes from woodland (pure) to grassland are similar in widely separated districts. In 1931 at an elevation of over 700 ft. a small wood of Scots Pine with an open growth had a grassy ground vegetation. The vegetation consisted of Sheep's Fescue (dominant), Creeping Soft Grass, Bent Grass, Meadow Grasses, Wood Sorrel (*Oxalis Acetosella*), Sheep's Sorrel, Mosses and Ferns. On the opposite side of the road there was a considerable extent of heathy grassland. This heathy grassland had originally been a Pine wood, for remains of the decayed stumps could still be found. There was a surface covering of rather peaty soil over a good red loam. The soil was acid (pH 4.9, lime requirement $2\frac{1}{2}$ –3 tons per acre). No manures had ever been applied and sheep were the only stock used for grazing. The area was a "grassland" dominated by Sheep's Fescue. There were also present Heather, Bent Grasses, Field Wood Rush, Heath Bedstraw (*Galium saxatile*), Mosses, Heath Rush (*Juncus squarrosus*) and traces of Common Rush (*J. communis*). The stage reached was a Sheep's Fescue-Bent grassland, with considerable patches of heath following the removal of the trees. Its relationship to the ground vegetation below the standing woodland is obvious. A still further improvement of the sheep-grazed area would soon change it to a Bent-Fescue grassland typical of many grasslands found in different parts of Britain. In both examples the position of the trees and stumps (and other points) indicated that the woods were not entirely natural and probably artificial. A very interesting example of transition from woodland to good grassland was found (1931) about a mile from the two examples already described. The "field" was originally a wood of Scots Pine which had been cut in 1917. By 1920 it was a dense growth of coarse vegetation with a high proportion of Field Thistles. It was then cut and heavily stocked with cattle, the ground being cut up by the heavy treading. The ground was then manured and sown with a seeds mixture, after which it was grazed and Wild White Clover seed was scattered by hand. The Clover grew and spread and the grassland improved. It was grazed by cattle and sheep in summer. In 1931 the vegetation which covered the ground consisted of 31 per cent. Wild White Clover, 30 per cent. Perennial Rye Grass, 20 per cent. Bent Grass, the remainder consisting of Crested Dogstail, Cocksfoot, Yorkshire Fog and Creeping Soft Grasses, Meadow Grasses, with a very small proportion of Field Thistles, Buttercups, Daisies, Plantains, Stinging Nettles and Docks. There was only a thin layer of peaty soil on the underlying red loam, which was beginning to show on the surface in parts of the area. The vegetation indicated that the "field" was potentially a good pasture carrying a considerable head of stock, comparable with some of the best pastures of the district. Traces of the old Pine stumps still remained, but they were largely disintegrated and not causing any inconvenience to stock.

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This example shows that it may be possible successfully to convert old woodland to good pasture at no great expense. In the present case the hard treading of the cattle was sufficient to turn up the soil, so that no ploughing was necessary. A careful examination of the area indicated that the wood was not natural.

Grasslands derived from moors. As already pointed out, some moorlands have originally been woods. The examples of grasslands now to be considered were all derived from one large area of moorland. The vegetation of this moorland chiefly consisted of the following plants: scattered trees of Scots Pine found in occasional isolated clumps; Juniper occurred but was not plentiful, but Silver Birch was plentiful in parts, and in one or two places slowly spreading: the ground vegetation was dominated by Heather, Dwarf Whin (*Genista anglica*) was common in parts: Sheep's Fescue, Wavy Hair Grass (*Desch. flexuosa*), Sweet Vernal and Bent Grasses were common; there were also present Devil's-bit Scabious, Bell Heather, Cross-leaved Heath (*Erica Tetralix*), Field Wood Rush (*Luzula campestris*), some Broom (*Cytisus scoparius*) grazed by sheep, Bird's Foot Trefoil (*Lotus corniculatus*), Crowberry (*Empetrum nigrum*), Bearberry (*Arctostaphylos uva-ursi*) and traces of Cotton Grass (*Eriophorum*), Deer's "Grass" (*Scirpus caespitosus*) and Moor Mat Grass (*Nardus stricta*). The first field examined consisted of Sheep's Fescue dominant, Bent Grasses (chiefly *Agrostis canina*) sub-dominant; also present, Tormentil (*Potentilla erecta*), Devil's bit Scabious, Mouse-ear Chickweed, Bird's Foot Trefoil, Wild White Clover, Yellow Rattle, Field Gentian, Ribwort Plantain, Eyebright (*Euphrasia*), Dog Violet (*Viola canina*), Tuberous Pea (*Lathyrus montanus*), Heath Bedstraw (*Galium saxatile*), and Ladies' Bedstraw (*G. verum*), Heather, Yarrow (*Achillea millefolium*), and traces of Crested Hair Grass (*Koeleria cristata*), Red Clover, Scottish Bluebell (*Campanula rotundifolia*), and Bearberry. In the grassy areas beneath and between Birches, Sheep's Fescue Grass was dominant and Bent Grass was sub-dominant: also present, Wavy Hair Grass, Tormentil, Bearberry, and traces of Heather, Sweet Vernal Grass, Crowberry and Devil's-bit Scabious. The areas near the Birch trees were all well grazed.

Adjoining the field just described was a permanent pasture also derived from the moor and never under the plough. The vegetation consisted of: Sheep's Fescue Grass dominant; Bent Grasses sub-dominant; Sweet Vernal Grass present in quantity; Bird's Foot Trefoil, Wild White Clover, Yarrow, Devil's-bit Scabious less plentiful; *Galium saxatile* and *G. verum*, Scottish Bluebell, Wavy Hair Grass (*Desch. flexuosa*) and Tufted Hair Grass (*Desch. caespitosa*), Ribwort Plantain, Eyebright, Ragwort, Germander Speedwell, Field Thistle and traces of Moor Mat Grass (*Nardus stricta*), Crested Dogstail (*Cynosurus cristatus*), Self-heal (*Prunella vulgaris*), Bracken, Birch, and dead remains of Heather. In this field were considerable patches of the viviparous form of Sheep's Fescue.

Another permanent pasture next the one just described had Bent Grasses dominant and Sheep's Fescue sub-dominant. There was an appreciable proportion of Wild White Clover, the field was good and well grazed and contained traces of the usual grasses found in sown grasslands, although it had never been under the plough or sown down to grass.

Grass fields which had been sown down and originally derived from this moor were quite typical of such fields. There was little if any evidence of the original flora occurring in the semi-natural fields. The long leys and permanent pastures of artificial origin (sown down) tended to be dominated by Bent Grasses with either Yorkshire Fog or Sweet Vernal Grass as sub-dominant. There was a fair proportion of Wild White Clover present, and occasionally Crested Dogtail was plentiful on the heavier soils.

Non-agricultural grasslands. The vegetation of a golf course just below Craigellachie Hill was interesting because it had originally been part woodland, part moor. The original wood had probably been Pine succeeded by Birch. Birch now clothes the slopes above the golf course. Beyond the Birch and at the edge of the course is Heather, and at the meeting of Heather and Grassland Moor Mat Grass occurs. The stocking with sheep was far more intensive on the course than any other neighbouring grassland area examined. The course consisted chiefly of a Bent-Sheep's Fescue Association. On the edge where grass was only occasionally or rarely cut, there was a considerable accumulation of dead stems and leaves. This was mixed with moss, which the taller growth seemed to draw up. After this process of accumulation has proceeded for some time, Heather appears and spreads. This was also noted in certain gardens some distance from the nearest moor or wood where the rough grass had been left derelict for many years. Another interesting feature was the change in the vegetation where a gateway was removed at the edge of the course to permit the sheep to enter a neighbouring area. On the course there were no young Birch trees or seedlings. On the other side of the fence there were plenty of seedlings and young trees, some already partially grazed. On the course Moor Mat Grass was fairly plentiful near the fence, but in the area beyond scattered young plants were just showing in a fan-shaped space opening out beyond the gateway. The spread of Moor Mat Grass in this new area was evidently due to sheep, since no other part showed any trace of the grass.

DISCUSSION.

It is obvious that the Spey Valley from Aviemore to Grantown-on-Spey has once been thickly covered by Scots Pine. Sessile Oak (*Quercus sessiliflora*) and a little Pedunculate Oak (*Q. robur*) had also grown, but there are few survivors or descendants to-day. Birch has been and is still plentiful, growing above or with Pines. Juniper is plentiful and generally occurs in open Pine woods, surviving long after the Pine has died out or has been cut. There are many records of the destruction of woodlands in the Spey Valley, both for

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purposes of war and for commerce. Destruction by fire of unknown origin is not rare, and even to-day occasional fires occur for which no definite cause can be given. Sparks from railway engines cause much damage in dry seasons where the railway passes through moors or woods. During 1933 the writer found burned areas in several parts of Scotland where the burning was confined to parts surrounding exposed outcrops of rock. The heat from the sun's rays raises the temperature of some of these dark rock outcrops to a dangerous height and doubtless explains at least some of the fires of 1933. There certainly were cases where it was difficult to attribute the causes to human agency. A severe fire may alter the vegetation of an area not only for many years but sometimes permanently. In some of the older woods to-day traces of fire many years ago can be found, and in such areas it is rare to find any Junipers except a few seedlings. Over many tracts, however, Pine has been cut and has not regenerated. Where peat has been washed away stumps of Pine could be found, and almost every stump examined showed no trunk near, while the smooth base and lack of trunks near by indicated beyond doubt that the tree had been cut, though in one or two instances it seemed that destruction had been by fire. To-day the constant burning of moors for game purposes successfully prevents natural regeneration of trees where this might occur. Frequently trees may be found at the edges of roads or near wet places where fire cannot do the same damage. The Pine stumps (in peat) are usually resting on gravel, sand, or broken rock, which suggests that the growth of the Pine is comparatively recent, much more recent than the Upper Forestian Period (8). There may be deeper peat deposits, but the writer did not note any beyond one example in the Spey Valley and a few further north. This is quite in keeping with some of the peat deposits near Edinburgh where Birch is found on boulder clay or gravel undoubtedly dating from the Upper Forestian Period (8).

Another interesting point was that remains of well-grown Pine trees were found at an elevation of approximately 2200 ft., far above any present local tree growth. Still more surprising was finding a solitary seedling of Scots Pine growing in the peat near their old remains. It is possible that if heather burning ceased the Scots Pine might recover some of its lost ground, although in some districts deer are blamed for preventing regeneration (5). Remains of Juniper were also recovered from the peat at the same locality.

It was noticeable that Bracken was not plentiful, and seldom showed strong growth in dense or even in many of the more open Pine woods. Where Birch occurred, however, Bracken was often plentiful and grew strongly. Birch and Bracken seem to grow very successfully together, since Birch does not seriously overshadow Bracken. The most luxuriant growth of Bracken found was in a Larch plantation outside the Spey Valley. This is also true of the south-west of England. These points were also referred to by R. Smith (11) when dealing with Perthshire.

In many parts Gorse or Whin (*Ulex europaeus*) is spreading and sometimes invading woodlands. This invasion is not confined to Gorse, for Broom (*Cytisus scoparius*) is now occupying considerable areas of light soil on agricultural land, and even successfully penetrating woods and spreading over moors. In one or two localities it is competing with, and had in one place overwhelmed Bracken. In one small plantation Broom had successfully captured the whole ground with practically no other vegetation beneath it.

As already pointed out, some at least of the moors are derived from old woods, and, but for grazing and occasional burning, would probably return to wood in time. In the case of many woods and moors, however, the grazing or biotic factor is important (1 (b)). The advantage of woods for grazing is obvious, since some shelter is available for animals in cold and wintry weather. On moors where grazing occurs at all it is generally just sufficient to prevent the growth of young trees and seedlings, while in woods the area is often much more restricted and undergrowth seriously affected. The result of this is that in woods grassland tends to develop often more quickly than on moorland, even though most of the trees are still standing. It is of course only in rather open woodland that stock are put to graze: in others there would not be sufficient keep. The transition to grassland from moor is often more slow and gradual, passing through several phases. There is generally a heath-grassland phase, as the writer recently showed (3). The first stage in the formation of grassland after this heath-grassland is generally the Sheep's Fescue-Bent grassland, which is followed by a Bent-Sheep's Fescue grassland. With still further improvement of the grassland Bent still remains dominant, but Yorkshire Fog, Sweet Vernal Grass, as already described, or even Crested Dogstail assume the sub-dominant position. It is not often that such grasslands reach the stage in which Wild White Clover is the sub-dominant species (practically second-class grassland (3)). The interesting and valuable feature of the changes recorded from either wood or moor to grassland is that they bear out in the reverse direction the findings of the writer for retrogressing permanent pastures in Devonshire (3). The same process also occurs in many districts during the breaking in of the land to agriculture. In some cases fields are still on peat, in others the peat has been all or partially removed for use as well as to improve the soil. The presence of Juniper in some of these fields is merely the last surviving trace of the woodland from which they are derived. The Berwickshire examples are in close agreement with these from the Spey Valley. The Trossachs is perhaps more like certain parts of England, but there is a marked similarity in the vegetation succeeding the woodland stage (1).

There was no time for soil examination, but for the most part the soils were light, sandy or gravelly, or at times a light loam, except where peat occurred. Where oaks were found there seemed to be a suggestion of boulder clay, for the soil was slightly heavier. The roads across some of the moors were metalled with material derived from large water-rounded stones dug out

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of the moor. Where rain washings from the moor road flowed on to the moor (Heather being dominant on the moor) the vegetation changed abruptly to a Bent-Fescue or Fescue-Bent type. These patches were closely grazed where rabbits occurred. This, and the fact that many of the plants recorded are not those of acid soils, suggests either that there is not marked acidity or lime deficiency, or there is no marked deficiency of bases, and that surface leaching is probably the chief cause of the rather poor surface vegetation. If grazing is controlled and not too selective, areas of Heather may become Bent-Fescue grassland. If the grazing animal is removed Heather will return in a remarkably short time (1 (a)).

Where Junipers occurred and grassland developed round them, the grassland invariably consisted of a vegetation with Bent and Sheep's Fescue as the dominant species. This is a feature that has been observed elsewhere (2). Further, the appearance of Juniper in grassland, especially on hill slopes, is very similar to what may be seen to-day in the Scottish Southern Uplands. In one or two localities in the Scottish Uplands it is known that Scots Pine and Heather were present before the land was broken in about one hundred years ago, and Oak has been found in the peat of the same area. Birch occurs in parts of the Southern Uplands, and in one or two localities is considered to be the remains of natural woodland. Bracken at times is very plentiful and troublesome, while its situation often suggests the sites of former woodlands. Considerable parts of the Southern Uplands of Scotland were formerly covered by woods forming part of the old Caledonian Forest. The changes traced in part of the Spey Valley are probably very similar to what has occurred in the Southern Uplands, where in many localities grazing of sheep over a long period is largely responsible for the prominence and certainly the spread of Moor Mat Grass in the grazing areas, thus greatly reducing the grazing value. The similarity of vegetation in various parts of the two areas is very noticeable. There is no doubt that grazing has been, and still is, an important factor in deciding much of the vegetation of the hills and semi-natural grasslands of Scotland as they are to-day.

It is evident from the examples given that in some cases trees are growing on good land which is much more suitable for agriculture than forestry. On the other hand, there are many so-called grazings where the yield of fodder for stock is so small that the ground would be much better occupied by trees. In the past there has often been a lack of discrimination in the utilisation of land. Now that the improvement of British agriculture is an urgent necessity it means a much more careful selection of land either for agriculture or forestry. Unfortunately, with the present tendency for arable land to be put down to grass, many of the older grasslands and even fields are rapidly becoming derelict. Many have already reverted to heath, scrub or woodland. If these old neglected grasslands are required again, reclamation will be a very costly matter and present planning might avoid heavy expenditure in the future.

On the forestry side progress in replanting is far too slow. There are considerable areas capable of producing sound timber which to-day are yielding practically nothing to the national wealth.

The dividing line where agriculture should cease and forestry begin tends to fluctuate with the economic conditions of a country. Yet, as indicated, there are places where the land is not good enough for agriculture and others where trees occupy potentially good agricultural land. To overcome this difficulty there must be more careful planning and some control. Before this can be effective, it must be preceded by careful surveys, which must include a botanical survey.

SUMMARY.

In the Spey Valley from Aviemore to Grantown-on-Spey Scots Pine is the dominant tree and has in the past dominated the vegetation of the valley and the slopes of the hills to at least 2000 ft. A few Oaks occur and some were coppiced, but Oaks are very infrequent. Juniper is an almost constant associate of open Pine woods either with or without Birch. Birch is frequent throughout most of the areas and in many places has replaced the Pine. Bracken seems to follow Birch in its spread. Some moors are derived from old woodlands, others never had trees. Further south in the Trossachs the Oak is dominant and Pine comparatively rare. Juniper is also infrequent. The Oak may have successfully captured this area from the Pine, but so far there is insufficient evidence to support such a belief.

The grassland development from woodland usually follows the same stages of "succession" in most districts, with the gradual invasion of grass into the heathy growth beneath the Pine trees. Sheep's Fescue is usually the first grass to gain dominance, with Bent Grasses sub-dominant. This is followed by Bent Grasses becoming dominant with Sheep's Fescue sub-dominant. The Bent Grasses remain dominant with either Yorkshire Fog or Sweet Vernal or Crested Dogstail sub-dominant. The grassland which develops from moorland follows the same sequence but generally shows a slower transition in its early stages, since the heathy grassland may continue for a considerable time before Sheep's Fescue and Bent Grasses gain the dominant position. In the deciduous tree region with Oak as the dominant tree there are generally more grasses in the ground vegetation and the transition is therefore not so varied and prolonged. Bent and Sheep's Fescue Grasses may at early stages gain dominance, so that grassland is virtually established before the trees disappear. Where there is treading and grazing of stock, especially cattle, the transition may be more speedy. In places a superior grassland may be developed, particularly when grass seeds are artificially sown.

From examples quoted, it is evident that the utilisation of land was not always judicious. To avoid this waste and unremunerative returns careful planning is necessary. This must be preceded by surveys which must deal

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not only with soils, elevation, aspect and climate, but also with the nature of the vegetation, past and present.

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THE MARINE ALGAE OF LOUGH INE

By T. KENNETH REES.

(*University College of Swansea.*)

(*With two Graphs in the Text and one Folding Map.*)

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I. INTRODUCTION.

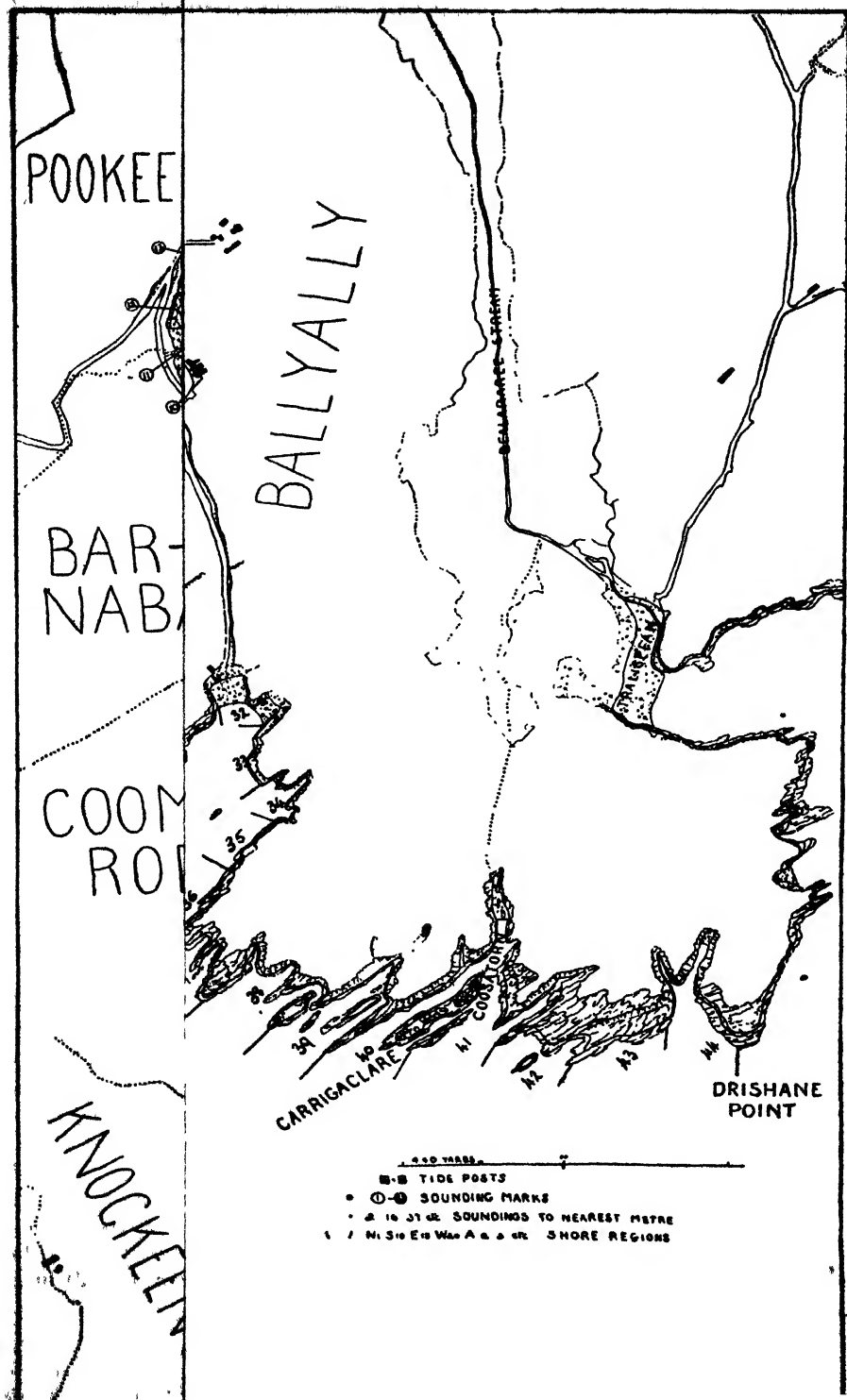
IN a previous communication (43), relating solely to the Phaeophyceae of Lough Ine, reference was made to certain preliminary work in connection with the general ecology of marine algae in this area. As a result of several subsequent visits, this work has been extended and the present paper embodies the results of the investigations carried out. Mention must be made, at the outset, of the great help and encouragement received from Prof. Renouf, the Director of the Marine Biological Station at Lough Ine, who has spared no effort to make working conditions the best possible under the somewhat primitive circumstances which prevail in this remote and isolated part of South Ireland.

II. DEFINITION OF AREA: METHODS OF INVESTIGATION.

The area investigated includes, in addition to the Lough itself and the creek leading to the open sea, a belt of exposed coast extending from Carrigathorna to Drishane Point, together with Tranabo Cove and the Coosh (see Map 1). It therefore includes habitats ranging from the exposed, gale-swept rocks to very sheltered and well-protected regions such as the Goleen in the south-west corner of the Lough. Visits were paid in June-July 1930, in August 1931, in July 1932, in March-April and late August 1933. In collaboration with Prof. Renouf, the shore has been divided into a number of regions for convenience in recording shore collections. These shore regions, totalling 177 in all, are distributed as follows:

Lough Ine: West side	38	Barloge Creek: West side	23
North side	12	East side	15
East side	20	Exposed coast: Bullock Island	6
South side	17	Carrigaclare	8
The Rapids: West side	3	Tranabo Cove	12
East side	2	Cloghan Islands	21

Owing to their steepness, and to the presence of a thick scrub of gorse, brambles and bracken above high-water mark, the rocks in many of these shore regions are only approachable by boat, and after preliminary exploration for suitable landing or mooring places, a considerable portion of the work was carried out from a boat (kindly lent by the Director). For collecting from the sub-littoral region use was made of (a) a hand razor securely tied at an acute angle to a long wooden pole; (b) a set of hake hooks attached to a weighted rope and to a scythe handle. A hand grab was also employed, and dredging resorted to upon occasions. Fortunately the water is, in the main, very clear, and by using a simple water observation glass (constructed by fixing a circular glass plate near the bottom of a tapering zinc cylinder) to counteract surface wave movement, an excellent idea of the main sub-littoral communities was



obtained, and representative collections were made as occasion required. In order to make the fullest opportunity of good weather for field work, and to devote the greater part of each visit to ecological problems, identification of doubtful and microscopic species was left until return to Swansea. A supply of previously labelled corked glass tubes of various sizes was always carried in the boat; unidentified plants were placed in them and upon return to the laboratory were transferred to similar bottles containing 2-4 per cent. formaldehyde in sea water, according to the size and structure of the alga. In addition, since many algal communities consist of minute filamentous species along with larger forms, representative samples of associations were frequently taken and examined at Swansea. Altogether 375 association samples were thus collected, and frequency determinations made in the field were checked by counts in the laboratory. Similarly, in order to obtain information regarding epiphytism, a large collection (over 400 samples) of plants bearing epiphytes was made and is now being investigated (see p. 129).

Finally, owing both to the clearness of the water and to the fact that a rowing boat was always in use, it was possible to work at any state of the tide, and rapid revisiting of areas for purposes of comparison was facilitated. The necessity, too, of examining areas in the littoral region both at flood and ebb tide, in order to evaluate the influences of ecological factors, and the need of penetration of caves whose sides are usually very steeply sloping, allowing no foothold, have been met by constant use of a boat. The writer feels that a false picture of the actual living conditions of littoral algae is often built up by those whose acquaintance with such an area is confined to visits when the tide is out. At least half such plants spend their lives more under submerged than under exposed conditions.

III. GENERAL PHYSICAL FEATURES OF THE AREA.

Attention has already been drawn to the main physical features of the area (Renouf (46)). Mention need therefore be made only of those which are of importance in algal ecology.

The Lough, which is roughly rectangular and about $\frac{3}{8}$ mile long by $\frac{3}{8}$ mile broad, consists in the littoral and sub-littoral regions of the following types of substratum:

(a) Rocks of Old Red Sandstone with occasional bands of Carboniferous slate and included quartz. They vary greatly in angle of slope and in dip and strike, but provide very few rock pools, although ledges are frequent at low water.

(b) Sheer walls, built of local stone or concrete, notably at the northern end of the Lough.

(c) Boulders and large flat slabs, especially along the lower western and much of the southern shore.

(d) Small flat or rounded pebbles forming beaches, scattered along each side, and sometimes cemented into a solid mass by calcareous algae.

(e) Mud banks, either of boulder clay overlying the rock, or where the soil is lapped by waves at high tide. These provide excellent limicolous communities of algae.

(f) Loose mud, very black and richly provided with humus, in deeper water off all four sides of the Lough, but most prominent in the Goleen.

The Goleen, which is a narrow southerly extension of the western side of the Lough, is especially interesting in that it shows a transition from a rocky and boulder substratum to a saltmarsh, richly provided with algal communities, with an extensive bed of *Zostera nana*, and influenced to some extent by the entrance of a small fresh-water stream (see pp. 114 et seq. and p. 123).

As has been pointed out by Renouf ((46), p. 418), the presence of a rocky sill in the Rapids has the twofold effect of reducing the extent of rise and fall of the tide in the Lough and of influencing the relative lengths of ebb and flow. The two accompanying graphs, for which I am indebted to Prof. H. N. Welsh (of the Engineering Department, University College, Cork), show clearly the difference between rise and fall of tide in the Creek and in the Lough. The following points are worthy of special note:

(1) The tide in the Lough continues to flow out, during spring tides, for about $3\frac{1}{2}$ hours after the outside tide has begun to rise. The total ebb is therefore about $9\frac{1}{2}$ hours.

(2) The rise of tide in the Lough occupies a little under 4 hours, and is accompanied by a considerable inrush of water, creating swift currents of fresh sea water, often a little turbulent; this effect is of great importance in influencing the distribution of many species in the Lough.

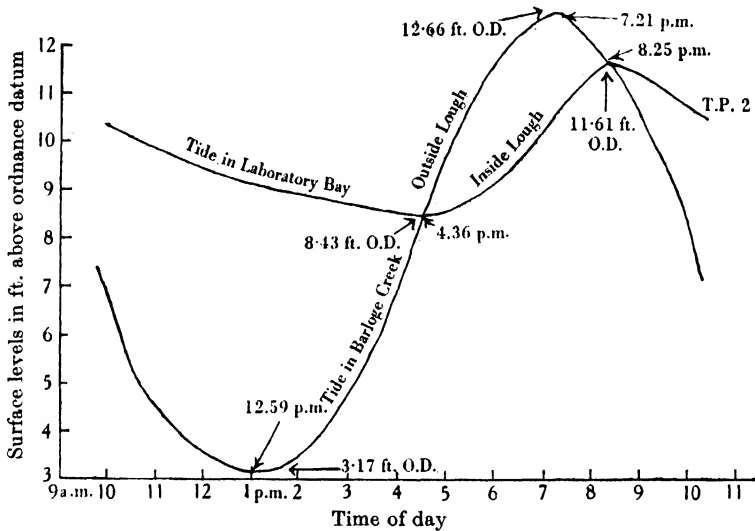
(3) During a period of neap tides, the outflow is even more prolonged, owing to the less rapid rise of water beyond the sill, so that the lowest ebbs in the Lough occur during the period when they are at their minimum outside.

Castle Island, which possesses rocky, boulder and pebble shores similar to the mainland, is interesting also in providing a second saltmarsh at a rather higher level than that in the Goleen. Its southern shore, facing the entrance to the Lough, receives some benefit from the inflowing water during flood tide.

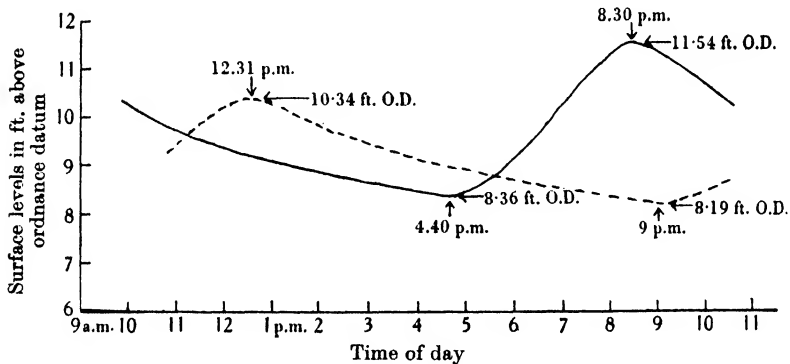
The Rapids. Except for a few seconds occurring twice a day, when the force of the incoming tide and that of the outflowing Lough water are balanced, conditions in the Rapids are those of constantly flowing and frequently turbulent water. There is therefore considerable strain upon attachment organs, and at the same time, owing to the full aeration of the water, the plants are richly supplied with oxygen and an ever-changing medium. It is not surprising, therefore, to find here several species normally confined to the exposed coast (see p. 123). The substratum consists of rocky ledges, boulders and flat stones

on the east side, and of a built wall on the west. The effect of differing angle of slope is well seen in comparing the two banks.

Barloge Creek. The Creek, which joins the Lough to the open sea, is about $\frac{2}{3}$ mile in length and can be divided into two very distinct regions: an upper



GRAPH 1. Comparison of rise and fall of tide in Lough and Creek on July 19th, 1932.
Outside rise = 9.49 ft. Inside rise = 3.18 ft.



GRAPH 2. Showing rise and fall of neap tide (interrupted line) and spring tide (continuous line) on July 11th, 1932 and July 19th 1932 respectively. Spring rise = 3.18 ft. Neap rise = 2.15 ft.

region stretching from the Rapids to the Coosh, and a lower region from thence to the open sea. The upper part exhibits the associations typical of sheltered bays, whilst the lower shows a series of transition stages between open-coast associations and those of sheltered areas. In addition, the presence of a series of narrow inlets on the western side, below the Quay, each bounded by rocks with a north and south aspect and varying greatly in angle of slope, results

in sudden discontinuity of predominant associations, and local aspect communities are a feature of this region. The presence of caves in this region will be dealt with later. The substratum in the lower creek is wholly rocky except for two inlets where boulders and flat stones predominate. The rocks descend sharply to a considerable depth and bear a good sub-littoral vegetation. Between the Coosh and the Quay, the floor of the Creek rises, and owing to the quiet conditions, the bottom is largely mud-covered and supports a *Zostera* and *Chorda* association. This muddy substratum continues up the greater part of the Creek, giving place below the Rapids to one of coarse sand and small stones. On the east side the mud overlies flat boulders and stones, but on the west is deposited on the projecting edges of steep rocks. In the Creek, therefore, there is a wide variation not only in the nature of the substratum, but also in the degree of exposure of its rocky sides. A further interest attaches to the lower creek by virtue of the presence of three small islands situated close to the east side. While too small to provide any measure of shelter to any region of the Creek, they show transitional associations similar to those found along the west side. The outermost island is of particular interest because of the presence of a number of channels of varying depth, running east and west, bearing a very rich growth of Rhodophyceae.

The exposed coast. The south side of Bullock Island (areas 18-23), the coast stretching from Tranabo Cove to Drishane Point (areas 36-43) and the headland at Carrigathorna have been investigated as typical of the exposed coast. In all cases the coast is rocky with a fairly steep and often sheer descent to the sub-littoral. There are many horizontal ledges due to division planes, but rock pools are infrequent. Several caves occur towards Carrigaclare and afford material for comparison with those in Barloge Creek. Considerable growths of mussels and barnacles occur throughout the exposed coast.

Tranabo Cove. Like Barloge Creek, the rocky shores of this cove show many transitions from exposed to sheltered types of algal communities. The chief interest of this cove is in the presence of flat sand-covered rocks in areas 25, 26 and 27, bearing many psammophilous genera. The Coosh, which separates the cove from Barloge Creek, consists of loose pebbles, covered at high water, fringed by boulders and bounded north and south by rocky ridges. It plays an important part in maintaining the quiet conditions of mid-Barloge Creek.

The caves. Six caves are present in the area, two fairly exposed ones on Carrigaclare, a deeply penetrating one on Bullock Island (area 16), and the other three at the back of the inlets Q., S. and U. on the west side of lower Barloge Creek. The degree of penetration of light and the angle of slope of the sides are the two determining factors affecting algal distribution in caves, and the six caves present many interesting differences which are fully dealt with later.

The saltmarsh. There are three saltmarshes in the area. The most important one consists of eight small islands of varying sizes, situated in the Goleen,

together with such portions of the mainland in the vicinity as are liable to be submerged at high tide. Owing to the general subsidence which is taking place along the whole south coast of Ireland, and to the accumulation of mud in the Goleen (due partly to currents and partly to deposition from the fresh-water stream) the water is gradually encroaching upon the marsh, which undoubtedly represents a phase of retrogression from a previously more extensive one. The mud washed away from the banks of the islands supports a *Zostera nana* association which lies all round the islands and mainland: the vegetation of this is largely a Juncetum and an upper general saltmarsh association. The sudden transition from Juncetum to Zosteretum has resulted in a great restriction of horizontal range for algal communities, which have become telescoped with much resultant overlapping. The second marsh, consisting solely of a Juncetum, with algal communities merely at the edge, occupies the greater part of the western extension of Cloghan Island. Its muddy banks pass almost vertically downwards to a rocky substratum. The third, a very small one, occurs in area E. 3, and again consists of a Juncetum with a few colonial and filamentous associations which are peculiar to saltmarshes in general.

IV. THE ECOLOGICAL FACTORS.

Every marine algal community has both a horizontal and a vertical range, the limits of which are determined by the interplay of two or more ecological factors. It is important, therefore, to examine the range of influence of each factor in turn before discussing their relative importance in the area under investigation. In a somewhat limited area it does not seem desirable to classify the factors into any main groups—a beginning will be made with those the effect of which is mainly upon horizontal distribution.

A. THE NATURE OF THE COAST.

The Lough Ine district possesses examples of exposed, sheltered and transitional habitats. The transitions may be gradual as in the Creek, or sudden as in Tranabo. The effect of exposure to gales, storms and the consequent surf-action is seen mainly in three directions:

(1) There is an upward extension of the upper limit of species growing at high-water mark. Bands of *Porphyra umbilicalis*, *Pelvetia canaliculata*, *Enteromorpha minima* and *Verrucaria maura* may on Carrigathorna and Gokane Point, reach 2–3 metres above their usual limit, although they never become extended upwards to the extent recorded by Börgesen for the Faeröes ((10), (11), pp. 693, 711).

(2) There is a great reduction of littoral vegetation both in species and in actual numbers, owing to difficulties in anchorage and germination. Much of the vegetation is of the encrusting type.

(3) There is usually a sub-littoral vegetation rich in Rhodophyceae, due to the richness of the water in oxygen and to the constantly renewed medium in which all save the lowest species live.

When, therefore, the contour of the rocky coast changes, or inlets, creeks or bays occur, affording shelter either to part or whole of the algal vegetation, the first noticeable change is in the lowering of the upper reaches of the upper littoral communities associated with a rich littoral vegetation, and the appearance of Phaeophyceae and even Chlorophyceae in the sub-littoral, which, apart from the Laminarias, continues to be populated largely by red algae. A detailed analysis of communities, together with the modifications and changes which they undergo, is given in the next section of the paper (p. 82). As the change from exposed to sheltered coast proceeds, the associations typical of the exposed coast give way to those peculiar to more quiet waters. The contrast between a typical vertical succession in each area is striking. Exposed coasts show: *Verrucaria maura* → *Porphyra* → *Bangia-Urospora* → *Callithamnion-Ceramium* → *Nemalion* → *Laurencia* → *Gigartina* → *Laminaria Cloustoni*. On sheltered coasts the sequence is *Verrucaria maura* → *Pelvetia* → *Fucus spiralis* → *Ascophyllum* → *F. vesiculosus* → *F. serratus* → *Gelidium* → *Laminaria saccharina* or *L. digitata*.

B. HYDROGRAPHIC AND OCEANIC FACTORS.

(1) *Movement of water.* Apart from the ebb and flow of the tide, to be considered as a separate factor, there is considerable movement of water influencing vegetation in various parts of the area. Along the south shore (areas S. 10–S. 17) and lower east shore (E. 11–E. 20) as well as along the south side of Castle Island (I. 9–I. 12) there is a steady flow of incoming and outgoing water, diverging from or converging upon the Rapids. The sub-littoral algae along the regions have their thalli constantly in motion and a luxuriant vegetation results, species like *Fucus serratus*, *Cystoseira granulata* and *C. ericoides* being practically confined to such regions. A similar steady flow is to be found passing down the middle of upper Barloge Creek, determining to a great extent the nature of the substratum. Where the flow is swift in the centre of the channel, coarse sand, gravel and shells are deposited, and bear a distinct association dominated by *Dictyota intricata* (see p. 109). Towards the margins of the Creek, the flow is much lessened, several quiet backwaters occur, and the substratum gradually changes to a muddy one overlying rocks and boulders. A vegetation typical of mud-covered rocks replaces that dominated by *Dictyota*. Near the Coosh, the mud brought down from the Lough meets a large volume of deep water in the lower Creek and is deposited in great depth, supporting the *Zostera* and *Chorda* bed. Wherever, between the Rapids and the Coosh, the flow of water is powerful, *Saccorhiza bulbosa* is prominent, and the growth of adjoining *Laminaria saccharina* plants

is luxuriant. A similar increased luxuriance of vegetation, due to water constantly in motion, is to be found on the projecting ledges of rocks running in an east or west direction along the west side of lower Barloge Creek. Around these ledges there is a constant swirl of water as the tide ebbs and flows, and their littoral and sub-littoral vegetation is more vigorous than that which grows on the north- or south-facing sides of the inlets which they delimit.

Turbulent water, which is spasmodic along the exposed coast, is constant in the Rapids and thus the determining factor of algal growth, which presents a marked contrast with that immediately above in the Lough and that immediately below in the Creek (see p. 123). Not only is there a thorough aerating of the water—itsself of importance in the constitution of the water of the Lough—but also a complete mixing of algal spores, which are swept along into the Lough with the incoming tide, thus in part accounting for the presence in the Lough of species out of their usual habitat (e.g. *Himanthalia lorea*, *Polysiphonia Brodiaei* and *Ceramium acanthonotum*). Tow-net catches from a boom projecting across the upper end of the Rapids show a great number of algal spores.

(2) *Temperature of water.* Variation in temperature at increasing depths (see Renouf (46), p. 420) is not itself of great importance in influencing algal distribution, for the significant figures relate to depths at which algae are absent or infrequent. It is, however, a factor of great importance in influencing seasonal migration of algae, and results similar to those recorded by Knight (37) and Rees (44) have been observed at Lough Ine (see p. 130). The water in the main is cold, and only becomes warm over mud in the Goleen, off Barloge Quay and the Coosh.

(3) *Salinity.* Decisive changes in salt content of the water affecting the nature and constitution of algal communities occur only at a few localities, in all cases associated with the entry of fresh water (particularly W. 26, W.1 and E. 2), but throughout the area fresh water may trickle down the rock or mud in the littoral region, and local societies dominated by Chlorophyceae and Myxophyceae occur (see pp. 83, 102, 112).

(4) *Rise and fall of tide.* There is little need to make more than a passing reference to the effect of this factor. Attention has already been drawn to the difference in rise and fall in the Lough when contrasted with the Creek (Renouf, (46), p. 419; Rees (43), p. 446), and the effect of this upon the vertical distribution of the Fucaceae. A similar telescoping is to be seen in the *Chondrus*, *Gelidium* and *Cladophora* zones. In the Lough itself, the very slight rise and fall (as little as 2.15 ft. at neap tide), with the consequent brighter illumination of the upper part of the sub-littoral region, may be the effective factor in preventing growth of the Rhodophyceae so prominent in this region in the lower part of the Creek, whilst at lower depths, to which, conceivably, they might descend, the muddy substratum and quiet water render conditions unfavourable for their growth.

C. CLIMATIC FACTORS.

(1) *The temperature and moisture of the air.* The Lough Ine district, in common with the south-west of Ireland generally, has an insular climate. Rainfall and stormy weather are frequent, and though during July and August prolonged spells of hot weather occur, the desiccation which the littoral algae might suffer is largely negated by the small horizontal range allowed by the contour of the rocks and by the profusion of growth, overlapping thalli affording effective protection against evaporation. The precipitation of rain undoubtedly affects the surface waters of the Lough, influencing the plankton: but here again, exposure to rain and fresh water, as to insolation, is lessened because the general steepness of the rocks allows little room for the lodgment of fresh water except in a few high-tide pools. In the Lough and Creek the plentiful growth of the Fuci gives almost complete protection to the sub-vegetation, and in regions where the Fuci tend to disappear, surf-action is a factor which must largely neutralise the effect of rain. It is notable that the whole of the north side of the Lough is poorly vegetated. Apart from the vertical wall in the littoral, and the pebbly substratum in the sub-littoral, both unfavourable to algal growth, the intense illumination of the shallow water may add to the general unsuitability of this region.

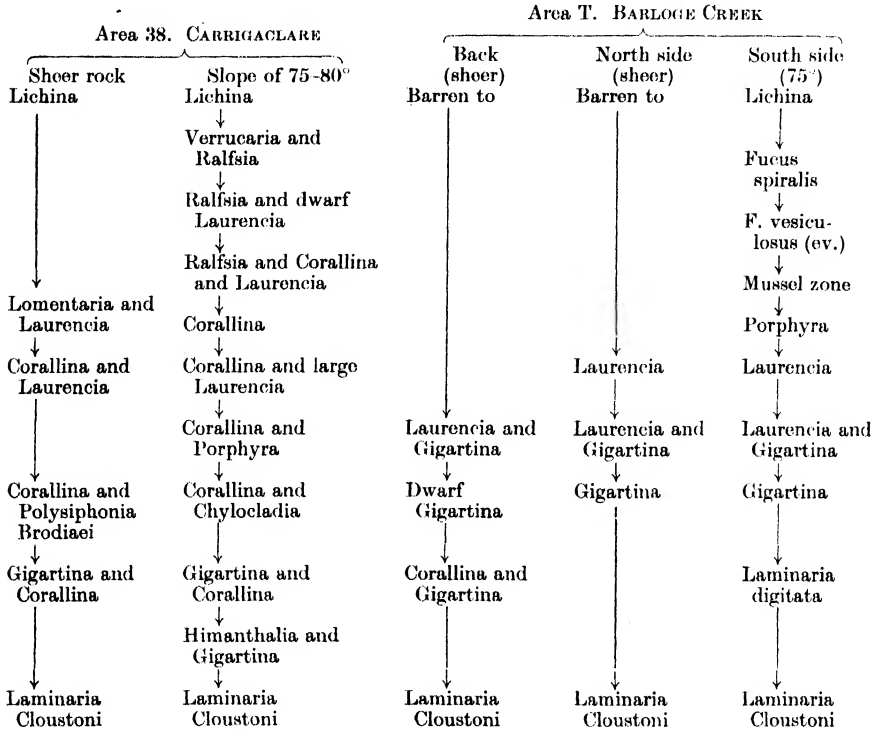
(2) *Light.* The effect of light as a factor influencing algal communities was not studied in any detail, but the observations made in caves and in deep water confirm the view of chromatic adaptation, but with numerous exceptions that call for autecological studies.

D. THE NATURE OF THE SUBSTRATUM.

Rocks, boulders, pebbles, sandy mud and mud all occur within the area and support a characteristic vegetation, whose constitution will be considered in the following pages. The main consideration is that of anchorage, and associations on all substrata save rocks tend to be discontinuous and patchy. Psammophilous and limicolous species replace the saxicolous wherever sand (e.g. Tranabo 25-27) or mud (e.g. Mid-Barloge: the Goleen) occur, and transitional communities such as those on muddy ledges or mud-bound pebbles are frequent. The part played by certain filamentous species in binding together sand and mud particles, and the change of form which saxicolous species undergo when they find temporary or permanent lodgment on such stabilised substrata, will be discussed later.

Aspect and angle of slope. The vegetation which occupies the surface of a cliff depends very much upon the aspect and the angle of slope. The more exposed south-facing aspects of the numerous inlets on Carrigaclare and along the west side of lower Barloge Creek bear a much poorer vegetation than the more sheltered sides facing north. While this is mainly due to surf-action, the increased exposure to sunlight experienced by a rock facing south must also

be borne in mind. Comparisons relating to aspect become complicated because of differing angles of slope. Many examples occur in which these inlets possess a vertical or even an acute-angled slope, and are barren of vegetation down to the *Laurencia* or even *Alaria* association; but with a slight change of slope, local societies occur in their appropriate zone. The following two examples are representative of many others:



The species which are able to find lodgment on vertical rocks are those which, like *Corallina*, *Lomentaria* and *Laurencia*, have a creeping basal portion which can become embedded in some minute crack or crevice, whereas the disc-like holdfast covers too small an area to allow adequate resistance to wave action. In more sheltered regions, as has already been discussed (Rees (43), pp. 447-8), the Fuci show varying ability to withstand increasing angle of slope, and a similar variability is found with their sub-vegetation, little save encrusting lichens, *Hildenbrandtia*, *Catenella repens* and *Gelidium* turfs being found on a sheer or acute slope. The two latter species have prostrate creeping basal portions from which the erect branches arise. Naturally, of course, any lessening of the angle of slope will increase the horizontal area occupied by a species.

reasonably treated from both the floral and algal point of view as a sub-formation. For the whole sea-coast algal vegetation, the term "panformation" may be suggested.

In the descriptive account which follows, the following abbreviations are used: H.W.M. for high-water mark of spring tide; L.W.M. for low-water mark of neap tides (base of littoral region); L.W.M.S. for low-water mark of spring tides.

(ii) DESCRIPTION OF COMMUNITIES.

A. OPEN-COAST FORMATION.

(1) Rocky subformation

(a) *Littoral region.*

(1) *Hildenbrandtia-Verrucaria association.* The similarity in growth form which characterises *Hildenbrandtia prototypus*, *Verrucaria* spp. and *Arthropyrenia* spp. has been considered by algologists sufficient justification for treating these genera as constituents of a single association. In the Lough Ine district the following species occur: *Hildenbrandtia prototypus*, *Verrucaria maura*, *V. microspora*, *V. mucosa* and *Arthropyrenia halodytes*. Of these *Verrucaria maura* is uppermost, existing throughout the area in broken patches or continuous bands at points as much as 2 ft. above the *Pelvetia* zone, and extending as a dull black paint-like incrustation through the *Pelvetia* zone into that of *Fucus spiralis*, and even, on boulders and flat sloping slabs, into the *Ascophyllum* zone. On vertical rocks its bathymetric range varies from 21 to 32 in., the lower 10 in. being often in scattered association with *Arthropyrenia halodytes*, which on boulders extends from mid-*Pelvetia* to the top of the *Ascophyllum* zone, and on steep rock surfaces may extend to L.W.M.S. *Arthropyrenia* is conspicuous in damp chinks and on quartz veins, and appears to prefer more shaded conditions than *Verrucaria maura* when occurring along with the latter. In places it merges into the mid-littoral *V. mucosa* zone, which is mainly developed on small pebbles, boulders or rocky surfaces which receive considerable protection from larger algal vegetation. *V. microspora* is only occasionally found, noticeably in scattered patches on gently sloping shores of flat slaty pebbles, and also in shallow pools associated with *V. mucosa*, whose distribution is always below that of *V. maura*. Wherever cracks, fissures or shaded areas occur in the rock, *Hildenbrandtia* is of frequent occurrence in the upper littoral region, but it may extend as an encrusting sub-vegetation on the underside or edges of pebbles to the edge of the sub-littoral. Where the fissures become mud-filled, *Hildenbrandtia* is replaced by *Catenella repens*. It is, moreover, a conspicuous inhabitant of the roofs and walls of caves, where it frequently lines the upper littoral reaches, and is an important component of the sub-vegetation with *Fucus spiralis* and *Ascophyllum* on bare rock surfaces. In sheltered localities it replaces *Lithophyllum incrustans* as a pioneer vegetation in shaded rock

pools near H.W.M. On very gradually sloping pebbly strands, and on very sheer rock surfaces, this association may be the sole vegetation until *Fucus vesiculosus* appears; and it is a conspicuous coloniser of newly bared rock surfaces or newly built concrete walls. Although best developed on moderately exposed coasts, it is a frequent inhabitant of sheltered bays, and is well developed along the shores of Lough Ine.

(2) *Upper association of Chlorophyceae.* The presence of a green band of varying width, dominated by *Enteromorpha intestinalis* near H.W.M., is a conspicuous feature of both exposed and sheltered coasts. Whilst its occurrence is normally determined by the presence of fresh water trickling down the rock surface or seeping through from vegetation above, it is not confined to such areas, and it may occur on exposed cliffs under normal conditions of salinity. On the open coast of Tranabo, the most conspicuous plant is *E. minima*, growing along with *Porphyra* and often completely monopolising mussel beds in this zone. On Island C. and on Carrigathorna, the loss of colour of both *Enteromorpha minima* and *Porphyra* during late summer gives to the rock ledges near H.W.M. a snow-capped appearance. With increasing shelter and with more frequent occurrence of fresh water, *Enteromorpha intestinalis* replaces *E. minima*, being at first very dwarf and tufted, but in damp fissures and in shallow pools, and with greater shelter, it reaches its normal development, and then forms a wide and conspicuous zone from the base of *Verrucaria maura* to about mid-*Fucus spiralis*. If the amount of water entering is sufficient to convert a trickle into a small stream, the *Enteromorpha intestinalis* zone may spread downwards to that of *Cladophora rupestris* near L.W.M., and may occupy almost the whole of the littoral region (e.g. S. 4, N. 12, E. 3, E. 25) and epiphytise any larger algae, such as *Fucus vesiculosus*, *Asperococcus fistulosus*, *Chondrus crispus*, etc., occurring in this region. In such cases there is usually some *Enteromorpha compressa* present. A remarkable local extension of this association occurs during late summer in areas O.-N., whose rock ledges and channels down to mid-tide level are covered by a Chlorophyceae association consisting of *Cladophora rupestris*, *C. pallida*, *C. sericea*, *Enteromorpha intestinalis*, *E. prolifera* and *E. clathrata*. The presence of a good deal of fine mud covering much of the rock surface (such mud-binding algae as *Rhodochorton floridulum* and *Gelidium pusillum* are also present) may account for the presence of *Cladophora pallida* and possibly of *C. sericea*, which is frequent on the muddy ledges of the Lough itself; but the upward extension of the two additional *Enteromorphas* is unusual. In a few places, especially in lower Barloge Creek, *C. rupestris*, which usually occupies a place lower down the littoral region, may form a joint association with *Enteromorpha intestinalis*, and in one area (S. 4) *Chaetomorpha litorea* replaces the usually dominant *Enteromorpha*. The whole association, both on exposed and sheltered coasts, may be taken to indicate low salinity, for even *E. minima* on exposed coasts must have to withstand a good deal of rain because of its high position on the rocks.

(3) *Porphyra association*. Along the exposed cliffs east of Tranabo, on the south side of Bullock Island and to the west of Carrigathorna, *Porphyra umbilicalis* occurs as a stunted, rather shrubby, growth in scattered patches below the *Lichina* zone. Further down it is replaced by the *Callithamnion-Ceramium* association, but is sometimes separated from this association by a band of mussels or barnacles. Its distribution on Carrigathorna, where it is largely confined to ledges facing landwards, seems to indicate that it cannot withstand extreme exposure to surf-action, but flourishes where breakers play over the rugged ledges. This inability to find suitable growth conditions may account for its patchiness along the rest of the exposed coast, where it occupies similar slightly protected ledges, but is absent from fully exposed cliffs. Although mainly confined to the upper littoral region, it may spread as an epiphyte on *Fucus vesiculosus* to mid-tide levels, and on mussels (a frequent habitat for the plant) it may spread down to the *Laurencia* association: it even occurs on Bullock Island epiphytically on *Corallina* and *Gigartina* at L.W.M. Minute plants frequently occupy fissures caused by joint or bedding planes. It is unusual to find it above H.W.M., except in minute tufts in fissures filled by salt spray. On the less exposed western shore of Barloge Creek, it is almost always bounded on the upper side by *Enteromorpha minima*, and may form a joint association with it as on Island C. The spring form of the plant (f. *linearis*) is abundant at the end of March, but unlike the Clare Island region, does not appear to extend upwards beyond the usual range of summer “*umbilicalis*” type. In spring *Porphyra* forms a joint association with the *Bangia-Urospora* society. Throughout the area plants are often densely clothed with *Acrochaetium secundatum*, and *Bangia fuscopurpurea* is not an uncommon epiphyte, with *Calothrix* spp. and *Lyngbya* spp. in autumn.

With increasing shelter its place is taken by *Fucus spiralis* and the upper part of the *F. vesiculosus* zone, but it occurs as an occasional constituent of the littoral flora of upper Barloge and even Lough Ine. The sandy-rock habitat so characteristic of its distribution along the coast of Wales occurs in Tranabo only, but no plants were found there. A remarkable local society, however, is found on boulders and projecting ledges below the sill in the Rapids, where well-aerated and turbulent water creates a medium not unlike that of the exposed coast, but here the plants instead of being stunted and shrubby are often several inches wide and float out freely in the swirling water. Apart from freedom from surf-action, the plants are exposed for little more than four hours each tide, and naturally become more luxuriant.

(4) *Bangia-Urospora society*. This upper littoral society appears to be a vernal one, for it was found only during the March-April visit of 1933. By the end of June it had disappeared, except that *Bangia* occurred as an occasional epiphyte on *Porphyra*. The three species composing the society are rarely all present together. A careful examination of several ledges revealed that *Bangia fuscopurpurea* has by far the widest vertical range, occurring on

barnacles and mussels above the *Porphyra* zone, and extending, especially on mussel shells, to mid-tide level. *Urospora isogona* occurs mixed with *Porphyra*, but more usually as a distinct belt below, especially when there are vertical sides to the ledges. It appears to favour exposure, being absent from pools and damp chinks shaded by *Porphyra*, but is abundant in such places below the *Porphyra* zone. Although apparently forming pure green sheets on the rock surface, it is in fact rarely quite pure, having a few associated threads of *Bangia* and of *Ulothrix flacca*. *Bangia*, on the other hand, is often quite pure as a fleecy covering on mussel shells below H.W.M., or colonising them jointly with *Porphyra*. The third constituent, *Ulothrix flacca* (with rare filaments of *U. pseudoflacca*) does not form distinct patches, but ramifies in variable amounts amongst the filaments of the other two species. The following vertical sequence, beginning at H.W.M. on an exposed ridge on Carrigaclare, is typical of the area:

Balanus and *Mytilus* bearing *Bangia* and minute Porphyras → pure *Porphyra* on *Balanus* and rock → damp channels dominated by *Urospora* in rope-like strands → sloping surface with *Porphyra* and *Urospora* codominant → pure *Urospora* belt on vertical sides of ledges → *Bangia* and *Callithamnion arbuscula* on mussels → *Bangia* on rocks and mussels to mid-tide level, spreading spasmodically to the *Laurencia* zone. Cotton has included *Enteromorpha minima* in this association, but its appearance throughout the year appears to justify its transference to the upper association of Chlorophyceae.

(5) *Association of Fucaceae*. The most interesting problem in connection with this association is the effect of increasing exposure to surf-action upon its component species, and since transitional regions between open and sheltered coasts are frequent, much evidence regarding this point has been accumulated. The upper part of Barloge Creek, protected by Bullock Island and Carrigathorna, may be considered a sheltered region. From areas G. to W., and from 9 to 17 a series of sudden changes occur, mainly because the northern and southern boundaries of the numerous inlets in the lower creek differ markedly in their degree of exposure to surf-action and in their angle of slope. Areas W.-Z., 18-23 and 37-43, may be considered as fully exposed coast, whilst Tranabo Cove shows transitional areas 24-26, and 36 to the fully sheltered 27-35. The problem is not a straightforward one owing to the interaction of three factors: (a) the degree of exposure to surf-action, (b) the angle of slope of the rock, (c) the degree of smoothness of the rock surface. A good deal of the exposed coast is barren of Fucaceae and bears only *Lichina confinis* and encrusting algae down to L.W.M. on sheer or almost sheer cliffs. The first of the Fucaceae to appear is *Fucus spiralis*, with a tough midrib and the spirally coiled lamina confined to the distal end. Once established, increasing shelter not only allows extension of its vertical range, but favours the development of the f. *platycarpus* which is the characteristic form of the plant in sheltered inlets. If, however, the very exposed cliffs bear small ledges

in the upper littoral region, the evesiculate form of *F. vesiculosus* (hereafter referred to as *F. ev.*) is the pioneer species, and on such ledges *Pelvetia canaliculata* may even appear before *Fucus spiralis*. Given therefore a suitable foothold, the dwarf and bushy evesiculate form of *F. vesiculosus* appears to be the species able to withstand the most fierce wave action. In this connection there is a marked contrast between 43-47 on the one hand and areas Z.-W. on the other, for off Drishane Point and Carrigaclare, *F. ev.* is definitely the first to appear as soon as the angle of slope is not too great and a small measure of protection is afforded by the rock ledges; whilst on Carrigathorna, with its much steeper cliffs and absence of ledges, *F. spiralis* always precedes *F. ev.* With increasing shelter *Pelvetia* becomes prominent and the vertical range of *Fucus spiralis* and *F. ev.* increase, the latter in time being replaced by the normal vesiculate form. *Ascophyllum* does not appear (except in one isolated sheltered region in the area U.) until area Q. is reached, and does not reach normal development as a zone above *Fucus vesiculosus* until the sheltered areas O.-N. On the moderately exposed areas H. and G. it is absent, reappearing again around the point F. With regard to *F. serratus*, if flat ledges are present at low water, it can withstand greater exposure than *F. vesiculosus*, but on vertical cliffs it is completely absent. As in the Lough, it only grows well where there is a constant but gentle flow of water, and it is absent from the quiet backwaters of Barloge creek.

Most of the inlets along the western shore of lower Barloge Creek have a northern and southern aspect, and the angle of slope is extremely variable. Where the rock is sheer, e.g. north side of area T., south side of area S., both north and south sides of area R., no Fucaceae appear at all, but with decreasing angle of slope (now no longer complicated by the exposure factor) first *Pelvetia* and *Fucus spiralis*, later *F. vesiculosus* and finally *Ascophyllum* appear, thus confirming the views already expressed regarding the effect of this factor in the Lough (Rees (43), pp. 447-8). Similar phenomena regarding both the effect of exposure to surf-action and of angle of slope are observable as the changes from exposed to sheltered conditions are studied in Tranabo Cove.

As the Fucaceae establish themselves in definite zones on the rock surfaces, characteristic sub-vegetation also appears. *Catenella repens* and *Hildenbrandtia* are frequent beneath *Pelvetia*, and may spread into the *Fucus spiralis* zone, which, however, except when fresh water trickles in, is usually devoid of any undergrowth. Beneath *Ascophyllum* such species as *Lomentaria articulata*, *Chondrus crispus*, *Gelidium pusillum*, *Plumaria elegans* and *Corallina officinalis* are to be found, while the upper part of the *Laurencia* association may penetrate into the *Ascophyllum* zone. Beneath *Fucus vesiculosus* and *F. serratus*, there is a sub-vegetation rich in shade-loving Rhodophyceae, e.g. *Lomentaria articulata*, *Membranoptera alata*, *Gigartina stellata* (see p. 90), *Laurencia pinnatifida* (see pp. 88-9), *Plumaria elegans*, *Ceramium flabelligerum*, *Rhodymenia palmata*,

Polysiphonia macrocarpa, *P. urceolata* together with such sand-binding algae as *Rhodochorton floridulum*, *Callithamnion roseum* and *Cladophora falcata* and encrusting algae of the *Hildenbrandtia* and *Lithothamnion* associations (see p. 91). The sub-vegetation found in more sheltered habitats is dealt with later in this paper (see p. 97).

(6) *Lichina association*. Cotton (23) has suggested that the two marine Lichinas, forming as they do an integral part of marine vegetation, should receive attention in an algal survey, and Knowles (38) regards them as a marine rather than a maritime group. Although not well developed in the Lough Ine area, the following notes will be of interest for comparative purposes. Both *Lichina pygmaea* and *L. confinis* are sporadic in appearance, extensive stretches of both exposed and sheltered coasts being devoid of both species. *L. confinis* occurs in a few parts on Drishane Point and on Bullock Island, at times extending downwards to the *Verrucaria maura* belt, but is not associated with any marine algae. *Lichina pygmaea*, which normally occurs above the *Fucus vesiculosus* and below the *Pelvetia* zone, is usually noticeable in the temporary absence of the Fuci. On many sheer rock surfaces, it is the only vegetation above the *Laurencia* association, or even above the *Alaria* belt. It inhabits both the bare rock surface and crevices, in which, because of their dampness, it reaches greater luxuriance. In more sheltered regions it is displaced by the thick growth of Fuci, but reappears here and there where the latter are sparingly developed on boulders, and together with encrusting species it may form a discontinuous band along several of the pebbly strands of Lough Ine. When occurring along with *Pelvetia* and *Porphyra*, it may spread upwards into the former and downward into the latter zone. Usually it is quite free from associated algae, but occasionally is found mixed with *Enteromorpha minima*, and it may bear epiphytes such as *Calothrix scopulorum* and *Lyngbya aestuarii*, especially if occurring along crevices containing fresh water. In Barloge Creek, during neap tides, it may remain uncovered by sea water for five or six days, and on sheltered sheer rocks it becomes very brittle with long exposure.

(7) *Callithamnion-Ceramium association*. *Callithamnion arbuscula* is definitely a species of the moderately exposed coast. It is found on Drishane Point, Carrigaclare, the south of Bullock Island and on Carrigathorna, but does not spread up the Creek farther than areas X. and 17. *Ceramium acanthotum*, with which it is frequently associated on these exposed cliffs, is, however, found spasmodically all along the Creek and is not uncommon along the north side of Lough Ine in clear water, inhabiting the shells and byssus of mussels. On moderately exposed rocks the two species form a well-marked belt lying slightly below that of *Porphyra*, and continuing downwards through the *Nemalion* zone to the *Laurencia* association of the lower littoral. The differences in relative distribution of the two members depend largely upon their essentially different growth forms. *Callithamnion*, with its almost upright

spongy stem and bushy habit, is found on limpet and mussel shells and on the rock surface, providing this is not too steep or smooth. *Ceramium*, with its finely branched and partially gelatinous thallus, occupies mainly crevices and damp chinks in the rock, and extends into shallow pools or epiphytically on other algae. The relative distribution of the two species, with regard to both exposure and substratum, can be followed on Island C. On the exposed southern aspect of this island, *Callithamnion* occurs below the *Porphyra* association, but may spread upwards into it along protected channels. Both *Callithamnion* and *Ceramium* are very scattered and confined to small depressions, eluding the wave-swept surface. On the more sheltered but still moderately exposed northern aspect they form a continuous zone, with *Ceramium* much better developed, but still confined to the numerous chinks, tiny crevices and pools, whereas *Callithamnion* now occupies the bare rock surface or grows on intervening shells. To some extent *Ceramium* is also epiphytic, growing on *Corallina officinalis*, which it follows downwards to the edge of the sub-littoral, whereas *Callithamnion* rarely descends below the top of the *Laurencia* association. The only associated algae are *Polysiphonia Brodiaei*, *Chylocladia ovata* and *Corallina officinalis*, with the following epiphytes on *Ceramium*: *Acrochaetium secundatum*, *Ulothrix flacca*, *Urospora isogona* and *Chaetomorpha tortuosa*. Of the two species, *Callithamnion* can withstand greater exposure, as is well seen on Carrigathorna, where on the north-north-east and south-south-west aspects both species are absent, but around the southern point *Callithamnion* appears some distance ahead of *Ceramium*. Although not actually connected with this association it is worthy of note that the *Ceramium acanthonotum*-*Polysiphonia Brodiaei* association occurs under *Himanthalia* in the Rapids, where the clear swirling water creates a habitat not dissimilar from that of the exposed coast.

(8) *Nemalion society*. During the summer months, at levels generally slightly below the last association, but occasionally ascending into it, a society of *Nemalion multifidum* (with rare *N. elminthoides*) is to be found. Its lower limit is usually sharply defined by the presence of a band of *Laurencia pinnatifida* below, but on Bullock Island it spreads through the *Laurencia* band to the *Gigartina* association below. Associated with the scattered *Nemalion* plants are *Halurus equisetifolius*, *Polysiphonia Brodiaei*, *P. macrocarpa* and *P. urceolata*. The *Nemalion* belt is frequently missing along exposed cliffs, and requires the presence of shallow ledges in the rock for normal development. An interesting telescoping of the *Callithamnion*-*Ceramium*, *Nemalion*, *Laurencia* and *Corallina* communities is to be seen on the southern face of Island B. On very exposed cliffs the *Nemalion* society is replaced by encrusting algae, and with increasing shelter in Barloge Creek its place is occupied by the *Plumaria*-*Ceramium* society to be described later.

(9) *Laurencia association*. Although easily recognised in the field, this association presents some difficulty in description because of its varying

character and the dissimilarity of the associated vegetation. On exposed coasts an almost continuous carpet of *Laurencia pinnatifida* is present near L.W.M., merging below into the equally prominent *Himanthalia* or *Gigartina* associations, or forming a sub-vegetation to *Fucus serratus*. In the transition to *Gigartina* an association with *Lomentaria articulata* is frequently formed, especially when overhanging ledges are present or some degree of protection is afforded either by *Himanthalia lorea* or by *Laminaria digitata*, with both of which *Laurencia* is associated as a sub-vegetation in the numerous channels running east-west along the south of Bullock Island and the Islands B. and C. In regions where there are flat ledges at low water, it may penetrate to the top of the *Laminaria Cloustoni* belt and thus enter the sub-littoral region. With regard to the upper limits, much depends upon the degree of exposure and the angle of slope. On many vertical exposed cliffs, *Laurencia* forms the first conspicuous algal zone below *Lichina* or *Porphyra*, the intervening rock being either bare or colonised by *Ralfsia clavata* and *Petrospongium Berkeleyi*. With equal steepness, but less exposure, it occurs below the *F. ev.* zone, and with less steepness but considerable exposure it lies just below the *Nemalion* belt, or, in its absence, the *Callithamnion-Ceramium* association, all three genera often penetrating into the *Laurencia* belt. On moderately exposed cliffs with a gradual slope, the belt widens considerably and penetrates upwards as a sub-vegetation to *Fucus vesiculosus*. With increasing shelter it is gradually superseded by the *Laurencia-Gelidium* association (see p. 100).

Although occurring on vertical rocks, it is best developed on gently sloping surfaces of rugged aspect, the hollows of which it fills and the channels of which it lines. On vertical rocks two growth forms are distinguishable: the uppermost part of the zone consisting of tiny prostrate thalli, often mixed with *Ralfsia* and *Corallina*, the lower part consisting of more luxuriant plants hanging down from prostrate thalli at the base. These two distinct sub-zones may be separated by an interpolated *Corallina* belt.

As is well known, *Laurencia pinnatifida* undergoes colour changes both with the season and with differing degree of exposure to light, as well as during the time of reproduction. During the months of July and August, much of the exposed *Laurencia* is yellowish or even yellowish green, thus giving a characteristic relief to the lower littoral vegetation, which on exposed coasts is predominantly deep red in colour. *L. hybrida* is not common, but during the Easter visit of 1933 was found frequently associated with *L. pinnatifida*, especially beneath *Himanthalia* and *Fucus vesiculosus*. Cotton reports that it disappears in May, but in three successive years it has been found in Lough Ine during July–August, and not improbably it may be another example of algal migration to which reference will be made later (see p. 130). With regard to other constituents of this association there is considerable variation depending upon the degree of shelter and the amount of light. On exposed coasts the following are frequent:

Chaetomorpha tortuosa
Cladophora sericea
Scytosiphon lomentarius
Punctaria plantaginea
Nemalion multifidum
Porphyra umbilicalis
Gelidium pusillum

Gigartina stellata
Lomentaria articulata
L. clavellosa
Chylocladia ovata
Polysiphonia Brodiaei
Pterosiphonia thuyoides
Callithamnion tetricum

Callithamnion arbuscula
C. granulatum
Ceramium rubrum
C. diaphanum
C. secundatum
C. acanthonotum
Corallina officinalis

Ceramium flabelligerum, *C. botryocarpum* and *Griffithsia flosculosa* appear with moderate shelter, and fringes of *Dictyota dichotoma* are frequent. The Chlorophycean growth, which in late summer becomes developed over *Laurencia* and other algae, will be referred to later (see p. 103).

(10) *Gigartina association*. The belt of *Gigartina stellata* which fringes the rocks of both exposed and moderately sheltered coasts, between L.W.M. of neap and spring tides, is a conspicuous feature of the Lough Ine district. It forms a natural lower extension of the *Laurencia* association wherever the latter occurs, and is itself limited below by either the *Alaria* or *Laminaria Cloustoni* belt. Although usually forming a limited or narrow belt, it may spread in sheltered inlets as high as *Porphyra*, and not infrequently into the *Fucus vesiculosus* zone. Where *Himanthalia* is present an interesting change of relative positions is noticeable. On moderately exposed rocks *Gigartina* lies mainly below *Himanthalia* and above *Laminaria Cloustoni*, but along areas Q.-N. *Himanthalia* lies in the main below *Gigartina*, which is limited above by the prostrate *Laurencia* turf-like association. A careful comparative study has revealed that it is *Himanthalia* which has altered its position rather than *Gigartina*, a peculiarity to be discussed more fully when dealing with the *Himanthalia* association. *Gigartina* evidently withstands exposure to air poorly, for its upward extension is always as a sub-vegetation to larger algae, and it not infrequently occurs, mixed with *Chondrus crispus*, in positions of total submergence. It can withstand greater surf-action than *Laurencia*, occurring on Carrigathorna and Carrigaclare in situations too exposed for *Laurencia*, but its extension through upper Barloge Creek towards the sheltered waters of Lough Ine is broken by the muddy-rock substratum, on which *Laurencia* continues to be well developed, though mixed with *Gelidium*. In the clear water of the Rapids (as a zone between *Fucus serratus* and *Saccorhiza*) and along the upper east and west shores of Lough Ine it becomes prominent again as a sub-littoral plant, evidently being intolerant of mud, but rarely forming a distinct zone or belt in sheltered regions, where it usually forms small discontinuous patches protected against strong light by the lower belts of the Fuci. Associated with *Gigartina* along exposed and moderately exposed coasts the following algae are to be found:

Dictyota dichotoma
Lomentaria articulata
Membranoptera alata

Cryptopleura ramosa
Callithamnion tetragonum
C. granulatum

Plumaria elegans
Polysiphonia urceolata
Corallina officinalis

and more rarely *Ulva lactuca* and *Cladophora sericea*.

(11) *Lomentaria society*. Although usually associated with the lower part of the *Laurencia* association and spreading into the *Gigartina* association,

Lomentaria articulata often forms local societies on its own account and seems worthy of treatment as a typical sciophilous alga of the exposed coasts. Wherever the rock beneath *Laminaria digitata*, *Himanthalia lorea*, *Fucus serratus* and *F. vesiculosus* possesses damp crevices or ledges with vertical sides, *Lomentaria* may be seen hanging down in festoons, its minute rooting articulations being embedded in division or bedding planes. It also occurs without such algal covering in small vertical channels or underneath overhanging ledges, and in such situations may spread to the sandy-rock sub-formation. At higher levels and in less exposed regions its place is taken by *Plumaria elegans*. Like *Gigartina* it is intolerant of mud and disappears in upper Barloge Creek, reappearing again as a shade and crevice alga in the Rapids, the walls of which on the western side, with their frequent vertical crevices, allow it abundant opportunity to develop.

(12) *Corallina*-*Lithothamnion* association. Along considerable stretches of the exposed coast towards Drishane Point, and to the west of Carrigathorna, the associations already referred to are missing or represented by a few isolated members. It is in such situations that *Corallina* and encrusting calcareous algae are most conspicuous. During the summer and early autumn the *Corallina* growth is very stunted and in the upper littoral region rather pale in colour, but in late spring the growth is more luxuriant and identification of the two species of *Corallina* is more easily possible. It is then evident that *C. squamata* occupies a higher zone than *C. officinalis*, occurring in wet fissures and pockets and in shallow pools or minute vertical channels from H.W.M. to mid-tide level, where its place is taken by *C. officinalis*, at first also confined largely to damp crevices and pools. Lower down it spreads over barnacles, mussels, and sponges as well as on the bare rock, and penetrates far down into the sub-littoral region. Associated with these two species of *Corallina* on these exposed rocks are *Lithophyllum incrustans* and *Lithothamnion Lenormandi*, and at low-tide level *Lithothamnion polymorphum*. They occur either as a sub-vegetation to *Corallina* or occupy damp places to its exclusion. *Lithophyllum incrustans* is the most prominent, especially in shallow sunlit pools. The whole association is one which cannot withstand drying, but maintains itself without conditions of shade, for large algae are completely absent here. With increasing shelter the encrusting species become less conspicuous, though *L. incrustans* still occurs on rocks along with other sub-vegetation, and it forms a basis for many patches of *Gelidium-Laurencia* turfs (see p. 100), while *Lithothamnion polymorphum* continues to be prominent in the sub-littoral. *Corallina officinalis*, however, is abundant throughout the area. It spreads at first into the *Callithamnion-Ceramium* and *Nemalion* associations, later entering the *Laurencia* and *Gigartina* associations. In the *Gigartina* belt it may form pure local societies in deep channels and may completely fill small pools. In more sheltered regions it seldom forms a belt but is intimately associated with other algae on sub-littoral muddy rock

ledges. It is an almost universal occupant of rock pools, except those near H.W.M.

(13) *Himanthalia association*. Next to the Fuci and Laminariaceae, no vegetation is so distinctive as the belt of *Himanthalia* at L.W.M.; even when in a purely vegetative state, its glistening olive-green "buttons" are visible for a considerable distance. Although, as has already been mentioned, it occurs in the Goleen, it is essentially a plant of the moderately exposed coasts, where it occurs either below the *Fucus serratus* zone, or, in the absence of the latter, below the zone of *F. vesiculosus* (including *F. ev.*). If the Fuci are absent it is found in the lower reaches of the *Laurencia* association which spreads as an undergrowth to the trailing receptacles. Its lower limit is sharply marked either by *Laminaria Cloustoni* or by a band of *Gigartina* intervening above the latter. The *Gigartina* zone may also become a sub-vegetation, and from Carrigaclare to area Q. it lies unmistakably below *Himanthalia*. Above area Q., however, *Gigartina* takes a position vertically higher than *Himanthalia*, which is followed either by *Laminaria Cloustoni* or *L. saccharina*, depending upon the degree of shelter afforded to the sub-littoral vegetation. *Himanthalia* is missing from the very sheltered areas M.-I., but reappears at H. and G., where surf-action is more apparent, disappearing again, except for isolated patches, in upper Barloge Creek. Just below the Rapids it is again prominent and continues there as a broad zone along the east side of the Rapids, extending along the east shore of Lough Ine as far as Castle Island and along the south shore, but is only really prominent on rocks in deep water at the entrance to the Goleen. Measurements taken to test its vertical position have revealed the fact that with increasing shelter it descends gradually to L.W.M.S., and except in the swirling water of the Rapids and along the east shore beyond, it assumes more and more a sub-littoral habit. On moderately exposed coasts surf-action lessens the degree of desiccation which a plant of the lower littoral region has to withstand, and with the gradual lessening of surf-action due to the increasing shelter afforded by the Creek, and the resultant danger of desiccation, *Himanthalia* sinks lower and lower until it becomes totally submerged with its fronds floating continually in the water. The fact that it does not establish itself in quantity in the Lough is probably due to its need of a constantly changing and fairly well-aerated medium, which it fails to secure in most of the Lough, though amply provided in the Rapids and along the lower east shore. On exposed coasts the only prominent epiphytes are *Ectocarpus velutinus*, *E. fasciculatus* and *Elachistea scutulata*; but in sheltered regions many epiphytes occur, including *Asperococcus fistulosus*, *Punctaria latifolia*, *Phylitis fascia*, *Dictyosiphon foeniculaceus*, *Sphacelaria cirrhosa* and *Ceramium rubrum*.

(b) *Sub-littoral region.*

(14) *Alaria association.* Bands of *Alaria*, from 2 ft. to 2 ft. 6 in. in depth, occur off Carrigaclare and along areas 17 and Y.-U. in Barloge Creek, as well as in patches on South Bullock Island, with an unexpected and quite discontinuous extension into area S. The plants always occur at the top of the sub-littoral, and are often associated with the presence of *Desmarestia ligulata* and *D. aculeata* below. It is usually succeeded by the *Laminaria Cloustoni* belt, through which it sometimes runs as a horizontal band and which it may displace altogether. If *Laminaria digitata* occurs, *Alaria esculenta* takes a place below it. The extent of the *Alaria* belt is too limited to study its distribution in relation to other Laminariaceae, but from its presence on exposed ridges, detached from the mainland, it appears to be able to withstand greater buffeting by waves than either *Laminaria digitata* or *L. Cloustoni*. On its lamina *Ectocarpus fasciculatus* is a frequent epiphyte, along with *Litosiphon Laminariae*, and on the basal part of the midrib *Callithamnion brachiatum*.

(15) *Laminaria association.* (i) *Laminaria digitata.* On exposed coasts this species is only found as a constituent of deep rock pools. On moderately exposed rocks it is confined to channels, mainly those running east and west, where it obtains some degree of shelter either through the depth of the channel or by protection afforded by outlying ridges. In such places it grows luxuriantly, the overlapping laminae covering a rich Rhodophyceae sub-vegetation of *Gigartina stellata*, *Laurencia pinnatifida*, *Porphyra umbilicalis*, *Corallina officinalis* and *Lomentaria articulata* (all intrusions from their respective zones), together with:

Chaetomorpha melagonum	Nitophyllum punctatum	Pterosiphonia complanata
Dictyota dichotoma	Cryptopleura ramosa	Halurus equisetifolius
Chondrus crispus	Chylocardia ovata	Plumaria elegans
Delesseria sanguinea	Lomentaria articulata	Callithamnion brachiatum
Membranoptera alata	Polysiphonia Brodiaei	Ceramium rubrum
Polyneura Gmelini	Pterosiphonia thuyoides	Lithophyllum polymorphum
P. Hilliae		

with rarer *Rhodymenia bifida*, *Phycodrys rubens* and *Plocamium coccineum*. Epiphytically on the stipe of *Laminaria digitata* the most common algae are *Acrochaetium secundatum*, *Callithamnion tetragonum* var. *brachiatum* and *Ectocarpus fasciculatus*.

With increasing shelter this species is no longer confined to damp channels, but spreads out as a belt at the top of the sub-littoral, beginning on flat projecting ledges, but later, with increasing shelter, occurring as a zone above *Laminaria Cloustoni* on surfaces that do not slope too steeply. It disappears wherever vertical rocks are found, and finally it occurs as a narrow belt in the swiftly flowing water of the Rapids, as a zone between *L. saccharina* and *Saccorhiza bulbosa*.

(ii) *Laminaria Cloustoni.* This species forms a continuous belt somewhat below the top of the sub-littoral on all fully exposed and moderately exposed

cliffs, being replaced by *L. saccharina* in sheltered bays. It is far more intolerant of exposure to air than *L. digitata*, and always occurs in well-aerated water. It descends to a depth of 10–12 metres and conceals a rich sub-littoral mixed vegetation, besides bearing many red algae as epiphytes, the following sequence of which is not uncommon on the surface of the rough stipes: *Rhodymenia palmata* with *Cladophora rupestris* and *Codium tomentosum* → *Polysiphonia urceolata* mixed with *Lomentaria articulata* → *Phycodrys rubens* and *Membranoptera alata* → *Heterosiphonia plumosa*, *Plumaria elegans*, *Hypoglossum Woodwardii* and *Rhodochorton parasitica* → *Polyneura Hilliae* → encrusting red algae, e.g. *Cruoria pellita*, *Petrocelis* sp., *Melobesia* sp., on the hapteron system. On the lamina *Ectocarpus Hincksii* and *E. fasciculatus* are abundant along with *Rhodymenia palmata*.

(iii) *Laminaria saccharina*. This alga only occurs in rock pools or in deep quiet caves on the exposed coast, but is abundant in sheltered regions, where it dominates a distinct association (see p. 104).

(iv) *Saccorhiza bulbosa*. This species is absent from the exposed coast except for a few scattered plants in the mouth of the Creek, but near area 15–13 and Tranabo 24 it becomes more frequent. It is mainly developed in the swiftly flowing water in and near the Rapids, where it becomes the dominant species, and spreads down as far as area F. wherever there is a flow of water. It is clearly a species for which a medium of constantly and swiftly flowing water is ideal, but it appears to be able to withstand somewhat muddy water much better than either *Laminaria digitata* or *L. Cloustoni*, for with sufficient depth it fringes the *L. saccharina* belt along both sides of upper Barloge Creek. Both in Lough Ine and in Barloge Creek it is gradually displaced in deep water by a *Chorda* association. Its epiphytes have already been mentioned (Rees (43), p. 442).

(16) *Sub-littoral association of Rhodophyceae*. The definite zoning of associations, under varying conditions, in the littoral region is no longer in evidence amongst the rich algal population dominated by *Laminaria Cloustoni* in the sub-littoral. The three main factors influencing the composition of this vegetation are (a) light, (b) angle of slope, and (c) the presence of mud or sand. The deepest vegetation seems to consist of calcareous algae such as *Lithothamnion polymorphum* and *L. compactum*, and non-calcareous species such as *Cruoria pellita* and *Cruoriella Dubyi*. The most frequently occurring thalloid species are:

Chondrus crispus
Plocamium coccineum
Membranoptera alata
Hypoglossum Woodwardii
Nitophyllum punctatum

Cryptopleura ramosa
C. ramosa var. *uncinata*
Polyneura Gmelini
P. Hilliae
Callophyllis laciniata

Callophyllis jubata
Rhodymenia palmata
Dilsea edulis
Callithamnion spp.

The less the angle of slope, the greater the number of species present. With the substitution of a muddy substratum for that of clean rock a total change occurs, and species similar to those listed later for the *Laminaria saccharina*

association are to be found. As far as could be ascertained the depth to which thalloid forms penetrate is about 10–12 metres. Although the Rhodophyceae predominate, a few Phaeophyceae also occur, notably *Desmarestia ligulata*, *D. aculeata*, *D. viridis* (rare), *Taonia atomaria* (inlets only), *Cutleria multifida* and *Chordaria flagelliformis*, together with abundant *Dichyota dichotoma*, both the normal form and f. *intricata*. A particularly broad form of *Dictyota* occurs as a frequent coloniser of small boulders in very deep water at the back of inlets or at the mouths of caves.

(c) *Pools and caves.*

(17) *Pool vegetation.* There are comparatively few pools on the exposed coast and only three which exceed 2 ft. in depth. The vegetation which they bear depends very much upon the season of the year when they are examined, and upon their depth, their position in relation to tide-level and the slope of their sides. They are of particular interest in relation to the problem of algal migration, and results obtained on the Welsh coast were confirmed in the Lough Ine area. In so far as they support a typical sub-littoral vegetation, of which they form an upward and discontinuous extension, they need not be dealt with here, and their transient seasonal population, though of the greatest importance for the species concerned, will be treated later in a paper dealing with the whole problem of over-wintering, seasonal periodicity and algal migration. The following is a summary of the outstanding features of pools of the exposed coast.

Pools above H.W.M., being largely brackish, are populated almost entirely by *Enteromorpha intestinalis*, with occasional Diatoms and *Ectocarpus* spp. A little farther down, about the level of H.W.M., shallow pools are entered by *Lithothamnion Lenormandi* and *Lithophyllum incrustans*, the latter forming pale pink sheets sometimes covering the whole bottom of shallow pools. *Ralfsia verrucosa* is occasionally found in such pools competing with *Lithophyllum*. *Scytosiphon lomentarius* and *Corallina squamata* are also frequent, the latter sometimes completely colonising the pool. Lower down, in the *Laurencia* zone, the predominating algae in summer are the Rhodophyceae, though in spring, species of *Ectocarpus* are prominent. Many of the pools are well shaded by the growth of *Gigartina*, dwarf *Laminaria digitata* and *Himantalia*, and contain the following algae:

<i>Chaetomorpha tortuosa</i>	<i>Scytosiphon lomentarius</i>	<i>Ceramium acanthonotum</i>
<i>Cladophora Hutchinsiae</i>	<i>Laminaria saccharina</i> var. <i>phyllitis</i>	<i>C. diaphanum</i>
<i>Enteromorpha compressa</i>	<i>Sphacelaria cirrhosa</i>	<i>Polysiphonia Brodiae</i>
<i>Ectocarpus confervoides</i>	<i>Callithamnion tetricum</i>	<i>P. macrocarpa</i>
<i>Ulva linza</i>	<i>C. arbuscula</i>	<i>P. nigrescens</i>
<i>Cladophora sericea</i>	<i>Ceramium botryocarpum</i>	<i>Corallina officinalis</i>

Almost all pools bear a fringe of *Corallina officinalis* near the edge, and of the remaining algae it may be said that their position depends largely upon the depth of the pool and the steepness of its sides. Near L.W.M. the small pools merge into the channels and bear the characteristic sub-vegetation to

Laminaria digitata already listed. The only really deep pool on the exposed coast is found in area 19, and its almost vertical sides bear the typical *L. Cloustoni* and Rhodophyceae vegetation present on sub-littoral rocks below. *Halidrys siliquosa*—a rare alga in the district—is found here, also *Bryopsis plumosa*.

(18) *Cave vegetation*. There are two important caves on Carrigaclare, a very fine one in area 16 and three smaller ones at the back of the inlets U., S. and Q. in lower Barloge Creek. None of them is fully exposed to the sea, but they obtain a considerable measure of protection from the inlet in which they occur or by their position in the Creek. Penetration of algae into the darker region of the caves rarely exceeds 10–12 yards, but a definite series of changes occurs both in the littoral and sub-littoral species. The cave in area 16 has been investigated on the occasion of each visit, and the following notes represent the main features. At the back of the cave, where it is intensely dark, no algae are found, the first signs appearing about 12 yards from the entrance where a dwarf form of *Plumaria elegans* is found in tiny cracks in the rock in the littoral region. The plants run along cleavage planes and little irregular contours in the rock. Associated with *Plumaria* is a monostromatic disc-like alga resembling *Erythrodermis*, but possibly only a sporeling stage of another species. With increasing light, *Plumaria* increases in size and amount, and becomes associated with *Ptilothamnion lucifugum*, which is often more frequent than *Plumaria*. Later a minute form of *Phyllophora epiphylla* appears scattered over the rock, both littoral and sub-littoral. About midway between the point where the first colonies of *Plumaria* occur, and the entrance to the cave, a copious littoral and sub-littoral growth begins to appear. In the littoral region the following occur in sequence from just about H.W.M.: *Hildenbrandia* → *Rhodochorton Rothii* → *Plumaria elegans* → *Lomentaria articulata* → *Phyllophora epiphylla* and *Corallina*, whilst in the sub-littoral region there are to be found:

Gelidium latifolium
Plocamium coccineum
Phyllophora Brodiaei
P. epiphylla
P. membranifolia
P. Traillii

Nitophyllum punctatum
N. uncinatum
Cryptopleura ramosa
Polyneura Hilliae
Delesseria sanguinea

Membranoptera alata
Hypoglossum Woodwardii
Pterosiphonia complanata
Dilsea edulis
Corallina officinalis

Nearer the entrance *Callophyllis laciniata*, *Callithamnion tetragonum* and *Rhodymenia palmata* var. *sarniensis* are found, and gradually the *Laurencia*, *Gigartina* and *Laminaria Cloustoni* associations of the Creek replace the cave vegetation.

In the other caves, though in the main similar to the one described, a number of features of interest occur. In both cave S., and in one of those on Carrigaclare, a very distinct band of the broad form of *Dictyota dichotoma* exists at considerable depth, lying on boulders or flat stones—in marked contrast to the f. *intricata* which is to be found hanging from the steep walls of

the inlets beyond the cave mouth. The view that the f. *intricata* is a deep-water form is not wholly true. In both cave S. and cave Q. there is a certain amount of mud which is collected into compact turf by *Rhodochorton Rothii*, *Callithamnion roseum* and *C. byssoides*, often associated with Myxophyceae typical of limicolous situations.

Mention should be made of the two very small caves which occur in region E. 3-4, in the Lough itself. Although their littoral and sub-littoral vegetation does not differ from that of the surrounding rocks, the effect of increasing shade on the somewhat heliophilous vegetation of this part of the Lough is quite marked, several bands ending quite suddenly in the cave entrance, e.g. those of *Cladophora rupestris* and *Gelidium*. *Hildenbrandtia* and *Rhodochorton Rothii* are plentiful on their roofs.

B. SHELTERED COAST FORMATION.

(1) Rocky subformation.

(a) Littoral region.

(1 a) *Hildenbrandtia*-*Verrucaria* association. Mention has already been made of the continuance of this association into sheltered parts (see pp. 82-3).

(2 a) *Upper association of Chlorophyceae*. The sheltered coast extension of this association has already been referred to (see p. 83).

(5 a) *Association of Fucaceae*. Factors influencing the distribution of Fucaceae in the Lough have already been discussed (Rees (43), pp. 443-8), but no reference was then made to the conspicuous epiphytic vegetation which they bear, nor to the nature of the sub-vegetation beneath their thalli.

Throughout the Lough, *Pelvetia*, when growing near muddy banks, becomes the host for a number of Myxophyceae, notably *Calothrix pulvinata*, *C. fasciculatus* and *C. confervoides*, whilst on the rock below *Hildenbrandtia* and *Verrucaria maura* are not infrequent. In the presence of mud on the rocks, the *Catenella repens* community may extend its upward range as far as the *Pelvetia* zone. *Fucus spiralis* is usually free from epiphytes, except for occasional tufts of *Elachistea fucicola*, and since there is not much shade afforded by its laminae the sub-vegetation consists mainly of *Hildenbrandtia* and *Verrucaria maura*. *Ascophyllum nodosum*, in addition to bearing copious growths of *Polysiphonia fastigiata*, may act as a host for *Ectocarpus confervoides* and *Pylaiella littoralis*, especially near fresh water. Its densely entangled fronds overlie a sub-vegetation of both encrusting and erect species. *Verrucaria mucosa* replaces *V. maura* on the rocks, and in damp chinks *Arthrogyrenia halodytes* is not uncommon. The *Cladophora*, *Gelidium* and *Catenella* associations frequently spread under *Ascophyllum*, and in sandy-mud areas, *Rhodochorton floridulum* communities are prominent. The following are the most common species below *Ascophyllum*:

<i>Ulothrix implexa</i>	oc.	<i>Gelidium</i> spp.	ab.
<i>Enteromorpha clathrata</i>	oc.	<i>Chondrus crispus</i>	oc.
<i>Cladophora rupestris</i>	fr.	<i>Laurencia pinnatifida</i>	fr.
<i>Ulva lactuca</i>	oc.	<i>Catenella repens</i>	fr.
<i>Cladophora flexuosa</i>	oc.	<i>Rhodochorton floridulum</i>	oc.
<i>Sphacelaria cirrhosa</i>	ab.	<i>Callithamnion roseum</i>	oc.
<i>Asperococcus fistulosus</i>	oc.	<i>Ceramium rubrum</i>	r.
<i>Leathesia difformis</i>	ab.	<i>Polysiphonia nigrescens</i>	r.
<i>Aglaozonia reptans</i>	oc.	<i>Corallina officinalis</i>	ab.

Beneath the thalli of *Fucus vesiculosus* a vegetation similar to that under *Ascophyllum* is found, except that *Cladophora rupestris* and *Chondrus crispus* are far more prominent. In contrast to *Ascophyllum*, it is densely clothed, near L.W.M., with a tangled mass of epiphytes of which *Dictyosiphon foeniculaceus* and *Asperococcus fistulosus* are especially noticeable during early summer. A total of forty-one epiphytes has been found, and as many as twenty-seven of these may occur on one individual. Not infrequently a chain of epiphytes is established, e.g. *Asperococcus fistulosus* growing on *Fucus vesiculosus* may bear *Dictyosiphon foeniculaceus*, itself bearing *Ectocarpus confervoides* upon which in turn filaments of *Bangia fuscopurpurea* may grow. This copious epiphytic growth is, of course, seasonal, but must act destructively to the host both by reason of its weight and by its interference with light. After stormy weather a high proportion of the plants washed up are those with heavy epiphytic vegetation. Before passing on to consider *Fucus serratus*, mention must be made of the *F. vesiculosus*-*Dictyosiphon* society which is a prominent feature in those parts of the Lough (e.g. W. 1, W. 34, E. 6, N. 12, I. 2), where a very gently sloping strand of small pebbles exists at and below L.W.M. *Dictyosiphon foeniculaceus* may occur as an epiphyte on *Fucus vesiculosus* or it may be free growing on the pebbles, on which it descends into deeper water than the *Fucus*, being replaced below by the *Stilophora*-*Enteromorpha* association characteristic of the deep water of the Lough. In this society such psammophilous species as *Gracilaria confervoides* and *Cladostephus spongiosus* are found, and *Brongniartella byssoides* is not infrequent. *Fucus serratus* is often covered by epiphytes similar to those found in *F. vesiculosus*, whilst its sub-vegetation consists largely of the upper limits of the sub-littoral associations, which, beneath the thalli of *F. serratus*, meet the *Gelidium* and *Chondrus* associations of the lower littoral region.

(6 a). *Lichina* association. Present in patches as already described (see p. 87).

(19) *Ulothrix* community. During spring and early summer an almost pure *Ulothrix* society is found in patches in the littoral region, especially on loose pebbles where the *Fuci* are absent or scattered. It was found in abundance near Barloge Quay (M.-L.) and on the pebble strand of the Coosh opposite during the Easter visit of 1933, but had disappeared by the end of June. *Ulothrix speciosa* is the dominant species, but is mixed with *U. flacca*

and *U. pseudoflacca*. Together they form thin uninterrupted sheets covering the pebbles and the gaps between them from the base of the *Pelvetia* zone to that of *Fucus serratus*, increasing in luxuriance in the lower littoral region, and often covering the stipes of such Fuci as may be present. The society spreads along the Creek in both directions as an epiphyte on *F. vesiculosus* and *Himanthalia lorea*. It does not occur on the rocks, but reappears again in quantity in Southern's Bay, though it is not conspicuous anywhere in the Lough. Its entire dissociation from the vernal *Bangia-Urospora* society of exposed coasts justifies its being treated as a separate community, for no trace of these two genera was found in the samples taken. Further, it occupies a position lower down the littoral region and is only developed in sheltered parts, whereas the *Bangia-Urospora* association is definitely one of exposed coasts. The occasional occurrence of *Ulothrix* threads as epiphytes on many littoral algae during summer and early autumn is probably due to the lingering on of isolated plants.

(9 a) *Laurencia association*. Although with increasing shelter the *Laurencia* association of exposed coasts gradually gives place to a *Laurencia-Gelidium* "turf," pure local societies of *Laurencia pinnatifida* are not uncommon in isolated regions of the Lough and upper Barloge Creek. They are frequently mud-covered and occur as fringes to flat stones in the sub-littoral region, or beneath the thalli of *Ascophyllum* or *Fucus vesiculosus*. In contrast to the association on exposed coasts, *Laurencia hybrida* is more frequent, especially in spring.

(20) *Plumaria-Ceramium association*. Although of limited distribution, the varied colour of this very mixed association renders it a distinctive feature of the littoral region of lower Barloge Creek. It develops best on steep or vertical rock surfaces on which the Fuci either fail to find a foothold, or are absent below the zone of *Fucus vesiculosus*, which, when present, forms the upper limit of this association. It is found along the east side of Island B., the south side of Island A. and in areas 16-13 and U.-P. in the Creek, but disappears on the more gradually sloping rocks of areas O.-N., where the greater growth of the Fuci, although allowing it at first some space as a sub-vegetation, eventually crowds it out. The association is really an aestival and autumnal one, developing upon the perennial substratum of *Laurencia pinnatifida*, and the varying colours are due to the local dominance of one or other of its constituent species. Where *Plumaria elegans* occurs, dark red (almost black) patches appear; with the presence of *Membranoptera alata* or *Ceramium rubrum* there are greenish yellow patches, whilst *Laurencia*, *Lomentaria articulata* and *Polysiphonia* spp. provide a brownish red background. Towards the lower limits of this association, *Laurencia* and *Lomentaria* predominate, and a *Laurencia-Leathesia* community leads to the *Himanthalia* belt. In a few cases, on vertical rocks, the association may reach to the top of the sub-littoral region, and is followed by the *Laminaria Cloustoni* zone.

The following species compose this association:

<i>Laurencia pinnatifida</i>	(with prostrate and pendant forms)	dom. as substratum
<i>Plumaria elegans</i>	ab.	
<i>Ceramium rubrum</i>	ab.	
<i>Membranoptera alata</i>	ab.	(a peculiar dwarf tufted form found in other places on littoral vertical rocks)
<i>Lomentaria articulata</i>	fr.	(especially at base of association)

together with scattered individuals of the following species:

<i>Codium tomentosum</i>	<i>Callithamnion byssoides</i>
<i>Isthmoploea sphaerophora</i> (on <i>Plumaria</i>)	<i>C. granulatum</i>
<i>Dictyota dichotoma</i>	<i>Ptilota sericea</i>
<i>Apoglossum ruscifolium</i>	<i>Polysiphonia urceolata</i>
<i>Callithamnion Hookeri</i>	<i>P. violacea</i>

The title *Plumaria-Ceramium* has been chosen, not because of any undoubted dominance of these two species, but because the most conspicuous colour changes depend largely upon their presence, and still more important, they are the last two species to disappear from the association, except for the perennial *Laurencia* and *Lomentaria*. Furthermore, as the association becomes replaced in more sheltered regions by that of *Laurencia-Gelidium*, both *Plumaria* and *Ceramium* extend into it far beyond any of the others. In the early phase of the development of this association, *Ceramium acanthotum* may play an important part, but it is quickly overcome by the developing sporelings of the other species during early summer.

(21) *Laurencia-Gelidium association*. As soon as the presence of mud or sandy-mud influences the rock surface in the Creek and in Tranabo, the *Laurencia* association of the clean exposed rocks is replaced by a closely matted turf dominated by a mixture of *Laurencia* and *Gelidium*. It is at first confined to crevices in the rocks, but later it spreads on to the rock surface from the base of the *Fucus vesiculosus* or *Ascophyllum* belt (into which on more sheltered rocks it spreads as a sub-vegetation) to the *Gigartina* or *Himanthalia* belt below. It is abundant on boulder beaches and pebble strands, creeping over the former and filling in spaces between the pebble strands. It is sometimes divisible into a pure *Laurencia* or a pure *Gelidium* sub-association, but it is more usual to find the two species together, thickly matted and densely interwoven. From a number of examples examined it would appear that either *Lithophyllum incrustans* or *Corallina officinalis* forms the basic layer on the rock surface, from which the other plants arise. The rounded basal calcareous discs of *Corallina*, which occur as whitish lumps, cover about one-third of the under surface of any piece of "turf" chiselled away from the rock. Between these discs the trailing prostrate portions of *Gelidium* spp. (mainly *G. pusillum*, *G. crinale* and *G. corneum*) occur, mixed with the calcareous lower branches of *Corallina*. Above this closely matted basal portion, the prostrate thallus of *Laurencia pinnatifida* is found, as a definite layer above the other two, but broken through by the erect branches of *Gelidium* and *Corallina*, which at this level tend to twist about and so create an upper matted surface from which the erect or pendant branches of *Laurencia*

then protrude. In some turfs *L. obtusa* may be present as well as *L. pinnatifida*. The net result is a multicoloured mud-retaining turf, gritty, calcareous and pale on the underside, richly red in the middle, and yellowish or pale red on top, depending upon the relative abundance of *Gelidium* or *Laurencia*. In parts this turf may present a more compact appearance due to the presence of *Rhodochorton floridulum* and *Ahnfeltia plicata*, while its upper surface becomes a nidus for many sporelings. The following species commonly find lodgment amongst its twisting prostrate layers:

Enteromorpha clathrata	ab.	Polysiphonia macrocarpa	r.
Dictyota dichotoma	oc.	P. nigrescens	oc.
Plocamium coccineum	oc.	Brongniartella byssoides	r.
Lomentaria articulata	fr. or l. dom.	(Leathesia difformis may form	
Callithamnion spp.	fr.	local patches of considerable	
Plumaria elegans	oc.	extent in late summer)	

As is natural, the mixed constitution of this turf leads to many local variations in its constitution and to a considerable range of epiphytic species. On flat ledges near L.W.M. dense colonies of *Leathesia* carpet this turf, especially if *Corallina* tends to dominate. It is often densely clothed with sponges and coelenterates, and offers a footing for the vegetative "buttons" of *Himanthalia*. In the Creek two changes are noticeable: (1) When the turf first appears (area 11-12) *Laurencia* is the dominant member, but with increasing shelter and a greater amount of mud, *Gelidium* encroaches more and more and may form an association of its own (see below). (2) As with *Gigartina* and *Himanthalia*, with increasing shelter, the lower limit of the association is extended and it enters the sub-littoral region in the Lough, though still mainly found as a sub-vegetation to the Fuci on rocks covered by sandy-mud. In upper Barloge Creek it is the main substratum for the lower association of Chlorophyceae, but here, as in the Lough, its place is often occupied by a *Gelidium* association.

(22) *Gelidium association*. With increasing shelter and the presence of more and more fine mud, *Gelidium* gradually replaces *Laurencia* as the dominant partner in the littoral turf association, and eventually forms either pure local patches, or more frequently continues in association with *Corallina*. *Gelidium corneum*, *G. pusillum*, *G. crinale* and *G. capillaceum* are the most frequently occurring species, though in deeper water and in shade, *G. latifolium* and *G. attenuatum* occur. The turf may be contiguous with that of *Catenella repens* or of *Rhodochorton floridulum* on muddy boulders and rocks in the *Ascophyllum* belt, and it extends downward through the mid-littoral Fuci to 3 or 4 ft. below L.W.M. (except on vertical rocks). It is abundant on flat ledges, in which case *Corallina* and *Leathesia* are prominent. In the clearer water along the north side of Lough Ine, *Gelidium* turfs occur in pure local patches in the clefts of the rocks or walls or fringing large slabs of stone in the upper sub-littoral. Both here and along the east and west shores of the Lough it is associated with the *Cladophora rupestris* belt, and along the south shore and

Goleen it forms along with *Corallina* a connecting band of vegetation between the lower Fuci and the *Stilophora-Enteromorpha* association of deeper water. This latter band is favoured by gently sloping surfaces, for on vertical surfaces it is missing both above and below L.W.M. A similar community exists along the south shore of Castle Island, with *Sphacelaria cirrhosa* and *S. radicans* as prominent partners in a close-matted turf. In the absence of larger algae below *Fucus vesiculosus* or *F. serratus*, these *Gelidium-Corallina* turfs support a very mixed algal population which is referred to later (see p. 109).

(23) *Chondrus society*. Wherever flat-topped boulders or flat projecting ledges appear at L.W.M. or slightly below, *Chondrus crispus* appears as a distinct society on moderately exposed coasts, e.g. lower Barloge Creek. It occurs below the *Gigartina* zone, fringing boulders, or growing erect from submerged rocky ledges. In such situations it is luxuriant and deep red in colour. Higher up the Creek, whilst retaining a similar habitat, it forms a joint community with *Corallina* and *Leathesia*, often replacing *Gigartina*, dominating the muddy ledges in much the same way as does *Gigartina* on more exposed rocks. In the Rapids, a *Chondrus* society appears prominently as an undergrowth to *Fucus serratus* and *Himanthalia*, and in the Lough occurs as a fringe to the *Cladophora rupestris* association or as a sub-vegetation to the lower littoral Fuci and to the lower association of Chlorophyceae. It is absent from sheer or steep rock surfaces and from the *Paracentrotus*-Encrusting Alga association. As elsewhere, *Chondrus* is remarkable for the great variety of forms and colours, and except when in fruit, it is not easy always to distinguish from the non-channelled forms of *Gigartina stellata*. Throughout the area it is essentially a plant of the upper sub-littoral region and is associated with such algae as *Membranoptera alata*, *Apoglossum ruscifolium*, *Cryptopleura ramosa*, etc., of the sub-littoral Rhodophyceae association.

(10 a) *Gigartina association*. The extension of this association into the Lough and upper Barloge has already been discussed (see p. 90).

(24) *Cladophora rupestris association*. Attention has already been drawn to the frequency with which *Cladophora rupestris* marks the entrance of fresh water on moderately exposed coasts. With increasing shelter it not only occurs in similar situations but becomes an almost continuous belt, gradually descending, until in the quiet waters of the Goleen it occupies the lowest littoral zone. Its ability to flourish where the water is slightly brackish is clearly seen in the vertical extension of the association which occurs wherever trickles of water run down the rock surface. Its presence as a lower littoral belt almost unbroken from W. 15 to W. 26 may be due to similar influences, for all along the southern end of the western shore fresh water either seeps out at high-tide level or forms trickles which flow over the littoral region when the tide is out. Similarly, along both the north and east shore, vertical extension of an otherwise narrow belt takes place in association with the entry of fresh water. Nevertheless brackish conditions alone cannot account for its distribution, for

it occurs in normal saline conditions in Barloge, and along stretches of the shore of Lough Ine which are without contact with fresh water. Assuming that its vertical distribution is determined by its inability to withstand much exposure to air, thereby limiting its occurrence to the lower littoral, the absence in the Lough itself of the thickly growing lower littoral *Laurencia* and *Gigartina* belts, may lessen competition and thus allow this bushy form to spread, whilst its very habit tends to the exclusion of other competing vegetation, and allows it to colonise pebbly strands equally with rocky surfaces. Plants of *Cladophora rupestris* frequently bear *Acrochaetium sparsum* as an epiphyte, and when this association occurs as a zone below *Fucus vesiculosus* or *Ascophyllum*, and above the *Stilophora-Enteromorpha* association, the following species are found: *Gelidium* turfs, *Chondrus crispus* (sometimes in joint association with *Gelidium*):

<i>Symploca hydroides</i>	<i>Enteromorpha clathrata</i>	<i>Apoglossum ruscifolium</i>
<i>Lyngbya semiplena</i>	<i>Sphacelaria cirrhosa</i>	<i>Rhodochorton floridulum</i>
<i>Cladophora flexuosa</i>	<i>Leathesia difformis</i>	<i>Dumontia filiformis</i>
<i>C. pallida</i>	<i>Asperococcus fistulosus</i>	<i>Polysiphonia furcellata</i>
<i>Enteromorpha ramulosa</i>	<i>Goniotrichium elegans</i>	<i>Ceramium arborescens</i>
<i>Monostroma</i> sp.		

In the quiet waters of the Goleen, where the association is almost continuous between the *Fucus* belt and the *Stilophora-Enteromorpha* association of deep water, the plants are densely clothed with epiphytes, as many as sixteen species, mainly Myxophyceae, being counted, including *Anacystis parasitica* and the rare *Elachistea Grevillei*.

(25) *Lower association of Chlorophyceae.* The lower littoral region of upper Barloge, and the west and south shores of Lough Ine show a clearly defined belt dominated by *Enteromorpha* spp. occurring below the zones of *Ascophyllum* and *Fucus vesiculosus*, or occasionally between them. To a lesser extent this lower association is found in lower Barloge Creek, where local patches or short belts of *Enteromorpha clathrata* and *Ulva lactuca* occur on *Laurencia*. In the Rapids it is represented by an *Ulva* belt below *Himanthalia*. Although presenting much the same general appearance there is a marked floristic contrast between the association in upper Barloge (areas F.-D. and 2-9) and that in Lough Ine. Whereas the former is dominated by *Enteromorpha clathrata* and *Ulva lactuca* (with only occasional *Enteromorpha compressa*), and grows epiphytically on *Fucus serratus*, *Laurencia*, *Gelidium* and *Gigartina*, the latter is dominated by *Enteromorpha intestinalis* and *E. compressa*, with scattered *E. crinita*, *E. prolifera* and *E. clathrata*, and is mainly saxicolous and narrower in vertical range. Differences in associated species also occur, a predominating number of those in Barloge being Rhodophyceae, whilst in Lough Ine the associated plants are mainly Chlorophyceae and Phaeophyceae. Both associations however, are transient, and at Easter, except for a little *Enteromorpha intestinalis*, there was no trace of either. In fact it may be said that towards the middle of July a wave of Chlorophyceae spreads over the Lough, and to a lesser extent the Creek, but has begun to wane by the end of August. The association of Chlorophyceae now described represents a more

stable localisation of this wave in areas where much mud is mixed with the pebbles and boulders, or lies thickly on the rock surface and its vegetation. Further, unlike the upper association of Chlorophyceae (p. 83), it bears no relation to the presence of fresh water.

(12 a) *Corallina-Lithothamnion association*. In sheltered parts this association is poorly developed, though *Corallina* continues to be a prominent component of the *Gelidium* and *Laurencia* associations, while *Lithophyllum lichenoides* is not uncommon along the south shore of Lough Ine. The deeper fruticulose *Lithothamnion* association will be described later.

(13 a) *Himanthalia association*. The extension of this association into Lough Ine has already been described (p. 93).

(b) *Sub-littoral region*.

(26) *Laminaria saccharina association*. On exposed coasts *L. saccharina* is confined to occasional deep pools and to deep quiet channels of sheltered inlets. The plant reaches its fullest development in the rather shallow slowly moving water of mid- and upper Barloge Creek, and along the south and lower east shores of Lough Ine, where again a steady but quiet flow of water is constantly maintained. In mid-Barloge Creek it gradually replaces *L. Cloustoni* as a sub-littoral fringing vegetation. In spring, when both *Chorda* and *Zostera* have died back, its distribution in this region can be clearly seen from Carrigathorna. On the gently sloping floor of the Coosh and Quay sides it forms a continuous band some distance below *Fucus vesiculosus* and *Himanthalia*, with occasional outlying patches in mid-Creek where stones large enough to give it anchorage can be found. With increasing steepness of slope of the sub-littoral rock surface, *Laminaria saccharina* gradually ascends to the base of the *Fucus vesiculosus* or *Gigartina* zone. In deeper water in mid-Creek it is replaced by *Zostera* and *Chorda*, the substratum being essentially soft mud, whilst on rocky substrata in upper Barloge, a band of *Saccorhiza* or even *Laminaria Cloustoni* intervenes between *L. saccharina* and the *Zostera* and *Chorda* fields which practically fill the middle of the Creek. As the Rapids are approached the distinction between small plants below *Fucus vesiculosus* and *F. serratus* and the luxuriant plants in deeper water becomes very evident; the latter extend up through the Rapids in channels between large boulders and continue as a sub-littoral band at somewhat deeper levels up the east shore of the Lough as far as the islands, and along the south side as far as area S. 11, though scattered individuals occur as far as the Goleen, off whose very steep east banks *Laminaria saccharina* becomes prominent again. As in Barloge, with increasing steepness of the rock, the plants reach increasingly higher levels on the rock and become contiguous with the lower Fuci, whereas *Chondrus* and *Cladophora rupestris* intervene on less vertical slopes. Although extending to very great depths on steep rocks (e.g. E. 17-18) it is replaced by the *Stilophora-Enteromorpha* association in the deeper waters of the Lough. Both in

the Creek and in the Lough a large number of algae are found in association with, but definitely dominated by, *Laminaria saccharina*. Detailed analysis is left for consideration until other sheltered sub-littoral associations have been described.

(27) *Cystoseira association*. In regions where the flow of water is not sufficient for the growth of *Laminaria saccharina*, its place as an association above that of *Stilophora-Enteromorpha* in deep water is taken by *Cystoseira granulata* and to a lesser extent by *C. ericoides*, which last is always the uppermost, rarely descends to a depth of more than 1 metre, and is better developed on gently sloping shores or rock ledges, than on the steep rock surface. It is chiefly found between S. 17 and S. 12, but occasional plants are found farther east and on the three small islands which connect Castle Island with the east mainland. *C. granulata*, however, may descend to much greater depths and form a joint open association with *Stilophora-Enteromorpha*. It is also frequently associated with the middle and upper part of the *Laminaria saccharina* belt. The fact that it extends as far east along the south shore as S. 2, and occurs in patches off the west shore, indicates that it can accommodate itself to conditions of less frequent water change than can *Cystoseira ericoides*, which occurs only in areas along which the main current of water entering and leaving the Lough would flow. Both species are often densely clothed with epiphytes (see Rees (43), p. 442). A third member, *C. fibrosa*, is rare, occurring only at the mouth of the Lough. In both the *Laminaria* and *Cystoseira* associations large plants of *Ulva lactuca* are of frequent occurrence.

(28) *Stilophora-Enteromorpha association*. During winter and early spring no conspicuous growth occurs in the Lough below the *Laminaria saccharina* and *Cystoseira* associations, but in early April a distinct though patchy association dominated by *Stilophora rhizoides* (and in deeper water by *Spermatocchnus paradoxus*) begins to appear, growing on small mud-concealed pebbles at depths considerably below the two perennial associations. Later on *Asperococcus bullosus* becomes a conspicuous member of this association, and toward the end of June, continuing until late August, species of *Enteromorpha* not only enter but even dominate it. The association spreads up into the *Cystoseira* association, which is very open and allows space for its development, and on flat or slightly sloping shores the two associations mix freely with each other, though always *Stilophora*, *Spermatocchnus*, *Asperococcus* and *Enteromorpha* occur as a distinct unit in deeper water. The species of *Enteromorpha* present consist mainly of the long tangled *E. clathrata* var. *Linkiana*, but other forms of *E. clathrata* occur along with *E. prolifera* and *E. crinita*. Unlike *Stilophora* these species may spread into the littoral region, notably during the Chlorophycean wave of late summer already mentioned. Along the north side of the Lough *Stilophora* is absent, but beginning in area E. 3 and W. 6 it continues to be a prominent member as far as the entrance to the Rapids, and into the Goleen. Although always attached to small pebbles, it appears to favour a muddy substratum, being absent on the clean slabs of the *Para-*

centrotus-Encrusting Alga association which so often intervenes between the *Cladophora* or *Chondrus* associations and the vegetation of deeper water. *Enteromorpha clathrata* may occur in pure mud, and is therefore found at greater depths on the muddy substrata of the Lough, and extends well into the *Zostera nana* bed of the Goleen, giving place there, however, to a *Chaetomorpha linum* society or to *Enteromorpha intestinalis* where fresh water enters at the extreme southern end. In addition to the species mentioned, the following are often found in this association:

<i>Ulva lactuca</i>	<i>Chylocladia kaliformis</i>
<i>Codium tomentosum</i>	<i>Hypoglossum Woodwardii</i>
<i>Cladophora utriculosa</i>	<i>Polysiphonia fibrillosa</i>
<i>C. albida</i>	<i>P. elongella</i>
<i>Sphacelaria cirrhosa</i>	<i>P. variegata</i>
<i>Asperococcus fistulosus</i>	<i>Antithamnion cruciatum</i>
<i>Cutleria multifida</i> var. <i>angustifrons</i>	<i>Ceramium tenuissimum</i>
<i>Chorda filum</i>	<i>C. rubrum</i>

while *Striaria attenuata* and *Pylaiella littoralis* are frequent in early summer. This association, which may be regarded as the limiting one in quiet waters, does not extend into the Creek, though occasional plants of *Stilophora* and *Spermatocnus* are scattered in the *Laminaria* and *Chorda* associations, especially where mud is present.

(c) *Pools and caves.*

(29) *Pool vegetation.* There are very few pools in Lough Ine itself. Those that occur at or near H.W.M. are entered by *Verrucaria microspora*, *Hildenbrandtia* and *Verrucaria mucosa*, and may bear a little *Enteromorpha intestinalis*. One medium-sized pool occurs in area S. 2 and bears *Lithophyllum incrustans*, *Chondrus crispus*, *Gelidium latifolium*, *Laurencia caespitosa*, *Polysiphonia nigrescens* and occasional *Enteromorpha clathrata*. A fairly representative set of pools at different levels is to be found in area V. in Barloge Creek. Although these are near the mouth of the Creek they are actually in a quite sheltered position. As is usual near H.W.M. the pools are colonised mainly by *Enteromorpha intestinalis*, but *E. paradoxa* var. *tenuissima* is not uncommon, bearing tufts of *Ulva lactuca*. In pools at slightly lower levels (about *Fucus spiralis* zone) which are usually deeper, dwarf *Codium tomentosum* and *Cystoseira granulata*, densely clothed with epiphytes, occur in addition to encrusting and tuft-like growths of *Sphacelaria cirrhosa* and *Corallina officinalis*. As an example of the wealth of species to be found in a single pool in the mid-littoral region the following analysis of the vegetation is given of one, 2 ft. 6 in. deep in the middle, and with gently sloping sides covered throughout by a close greenish turf of *Corallina officinalis*, *Gelidium pusillum*, *Sphacelaria cirrhosa* and *Lithophyllum lichenoides*.

MYXOPHYCEAE		
<i>Calothrix consociata</i>	<i>Calothrix confervicola</i>	<i>Rivularia atra</i>
CHLOROPHYCEAE		
<i>Enteromorpha clathrata</i>	<i>Cladophora rupestris</i>	<i>Cladophora albida</i>
<i>Ulva lactuca</i>	<i>C. pallida</i>	<i>C. arcta</i>
<i>Chaetomorpha litorea</i>		

PHAEOPHYCEAE

Sphacelaria cirrhosa
Asperoooccus fistulosus
Myriotrichia claviformis

Myriactis pulvinata
Elachistea flaccida
Leathesia difformis

Laminaria digitata
Himanthalia lorea
Cystoseira granulata

RHODOPHYCEAE

Acrochaetium Daviesii
Chondrus crispus
Gelidium pusillum
Laurencia pinnatifida

Pterosiphonia fruticulosa
Brongniartella byssoides
Ceramium rubrum

Peyssonnelia Harveyana
Lithophyllum incrustans
Corallina officinalis

One feature of ecological interest in this and neighbouring pools at the same level is the fringing zone of *Cladophora rupestris*, which replaces that of *Corallina* of more exposed pools, and it is noteworthy that the position of *Cladophora* in the pool is closely paralleled by its occurrence as a band at or just below L.W.M. in the Lough. Further, the general wave of Myxophyceae development in early autumn and that of the Chlorophyceae in late summer is reflected also in the vegetation of rock pools.

(30) *Cave vegetation*. Already described (see pp. 96-7).

(2) Sandy and/or muddy-rock subformation.

(a) *Littoral region*.

(31) *Rhodochorton association*. In view of the presence of muddy-sand in Tranabo Cove, in the mid- and upper parts of Barloge Creek and in Lough Ine itself, it is somewhat surprising not to find a more extensive area colonised by *Rhodochorton floridulum*, which only becomes extensive on the sandy islets of West Tranabo. To some extent this may be due to the steepness of the rocks elsewhere. Few flat ledges of any extent are found and there is little chance for the accumulation of sand or mud. The association is best seen in spring, before it becomes carpeted by the numerous transient plants of early summer. It has a wide vertical range, occurring on boulders in mid-Barloge at the *Fucus spiralis* level, and it is a frequent though very localised sub-vegetation to *Ascophyllum* and *Fucus vesiculosus* on flat slabs and boulders in upper Barloge Creek. It may spread as an undergrowth to both *Laurencia* and *Gelidium* turfs and may enter the sub-littoral on sloping muddy rocks or slabs in the quiet backwaters of areas 2-9. In Tranabo (areas 24 and 25) it forms a compact sandy carpet over the flat underlying rock at low water, but spreads upwards as far as the *Ascophyllum* zone along sheltered channels or fissures in the rocks. In the main it is a pure association, though in local patches *Sphacelaria cirrhosa*, *Callithamnion roseum*, *Cladophora lanosa*, *Ceramium ciliatum*, *C. strictum* and *Gelidium* spp. occur, and undoubtedly aid in the process of sand-binding. According to season a large number of sporeling plants develop on the sand thus bound, but few erect species are found, the following being most evident: *Cladostephus spongiosus*, *Chondrus crispus*, *Gigartina stellata*, *Laurencia pinnatifida* and *Ahnfeltia plicata*. This association at higher levels is usually replaced by the *Catenella* and general limicolous association to be described later.

(32) *General association of sandy-mud-covered rocks.* The flat sandy-mud-covered lower littoral and sub-littoral rocks which stretch out in bays 24, 25, and to a lesser extent in bay 26, in Tranabo Cove are bounded on the north and south sides by rocky ledges, and are backed by a small sandy beach. These rocks bear a large number of species, no one of which is clearly dominant. The *Corallina-Cladostephus* association mentioned by Cotton (23) does not stand out conspicuously, and in the absence of any clear distinction of zones or communities, a list of species found there on three successive visits is given below:

<i>Symploca hydroides</i>	(local)	<i>Gelidium pusillum</i>	oc.
<i>Cladophora pallida</i>	oc.	<i>Membranoptera alata</i>	oc.
<i>C. sericea</i>	oc.	<i>Acrosorium reptans</i>	r.
<i>Ulva lactuca</i>	ab.	<i>Nitophyllum punctatum</i>	r.
<i>Codium tomentosum</i>	oc.	<i>Laurencia pinnatifida</i>	ab.
<i>Sphacelaria radicans</i>	ab.	<i>Chondria dasyphylla</i>	oc.
<i>S. cirrhosa</i>	ab.	<i>Polysiphonia nigrescens</i>	r.
<i>Asperococcus fistulosus</i>	oc.	<i>Pterosiphonia thuyoides</i>	r.
<i>Leathesia difformis</i>	fr.	<i>Rhodochorton floridulum</i>	ab.
<i>Mesogloia vermiculata</i>	oc.	<i>Ceramium rubrum</i>	oc.
<i>Chordaria flagelliformis</i>	r.	<i>C. ciliatum</i>	oc.
<i>Cladostephus spongiosus</i>	fr.	<i>C. echinotum</i>	oc.
<i>Pylaiella littoralis</i>	oc.	<i>C. acanthotum</i>	r.
<i>Colpomenia sinuosa</i>	oc.	<i>Chondrus crispus</i>	fr.
<i>Aglaozonia reptans</i>	r.	<i>Gracilaria confervoides</i>	fr.
<i>Acrochaetium virgatulum</i>	(ep.)	<i>Rhodymenia palmata</i>	oc.
<i>A. Daviesii</i>	(ep.)	<i>Chylocladia ovata</i>	oc.
<i>Gelidium coreum</i>	oc.	<i>Corallina officinalis</i>	ab.

The *Gelidium* spp. sometimes form small local tufts, while *Laurencia*, *Symploca* and *Rhodochorton* occur usually in small local societies where the sand is not very deep. The lower limit of the association is determined partly by the *Chorda* association on mud, and partly by the fringing *Laminaria* belt on the more sharply descending rocks beyond. In connection both with this association and with that dominated by *Rhodochorton* there is evidence of a good deal of change year by year in the amount of sandy-mud actually bound together by the psammophilous species. Three areas were mapped out by reference to well-marked rock features, each half a square yard in area, and the amount of sand bound by *Rhodochorton* was estimated. The following table shows totals to the nearest 10 sq. in. for 1931, 1932 and 1933, in the latter year Easter and July.

	Area 1	Area 2	Area 3
1931	336	268	450
1932	402	221	552
1933 Easter	432	200	416
July	437	210	443

It is evident that the rate of colonisation by *Rhodochorton* may be as much as 15 per cent. of an area during the year, but that the sand-binding action is often neutralised by erosion during gales. A similar experiment in Gower (Glamorganshire) has shown that on raised rock surfaces the loss by surf-action is very little, but that *Rhodochorton* associations bordering a sandy stretch change markedly year by year.

(b) *Sub-littoral region.*

(33) *Pebble and boulder association and muddy ledge association.* In Tranabo (area 24), in lower Barloge (area W.), and more conspicuously in Lough Ine, there are local sheltered areas in the sub-littoral region where the substratum consists of pebbles of various sizes or of small boulders with a good deal of sandy-mud both on their surfaces and filling the spaces between them. They bear a varied assortment of sub-littoral species, the occurrence of which naturally depends upon the season of the year and the clearness of the water. A similar very general assortment of species is to be found on mud-covered rocky ledges or somewhat angular boulders such as are found around Castle Island. The species composing these associations are either attached to the rocks and pebbles or more often to *Laurencia-Gelidium*, *Corallina* or *Sphacelaria* turfs. The table on pp. 110–11 gives comparative lists for six areas of this nature.

(34) *Fruticulose Lithothamnion association.* The presence of an abundance of calcareous encrusting species in the sub-littoral region of the Lough, and their scarcity in the Creek, have already been commented upon from the biological point of view (Renouf (46), p. 420). Further, their association with *Paracentrotus lividus* on gently sloping flat stones appears to result in conditions impossible for other algal growth, and almost startling transitions between copious algal growth and its complete absence occur within a single foot along parts of the south and west shores and in the Goleen. A report on this biotic problem is in preparation and will include a full treatment of the fruticulose Lithothamnion of the Lough. Mention is here made of the association in order to give completeness to the general treatment. The following species occur: *Lithophyllum polymorphum*, *L. fasciculatum*, *L. incrustans* (all three with peculiar varieties), *Lithothamnion calcareum*, and *L. compactum*. This association is found in quiet waters with absence of mud and undergoes many variations in floristic and morphological constitution.

(35) *Dictyota intricata association.* The centre of upper Barloge Creek, along which the outflowing water from the Lough passes swiftly but without turbulence, is occupied by gravelly substrata, the formation of which has already been referred to (see p. 76). Opposite Southern's Bay the water is shallow enough to wade into from a boat, but reaching greater depths lower down the Creek it is occupied by a very open association in which the dark brown tufts of *Dictyota dichotoma* var. *intricata* are the most frequent and conspicuous. Associated with it are the following:

<i>Ulva lactuca</i> var. <i>latissima</i>	<i>Hypoglossum</i> <i>Woodwardii</i>
<i>Enteromorpha clathrata</i>	<i>Membranoptera alata</i>
<i>E. crinita</i>	<i>Cryptopleura ramosa</i>
<i>Ectocarpus confervoides</i>	<i>Callithamnion tetragonum</i>
<i>Mesogloia vermiculata</i>	<i>Antithamnion plumula</i>
<i>Colpomenia sinuosa</i>	<i>Griffithsia flosculosa</i>
<i>Stilophora rhizoides</i> (with epiphytic <i>Elachistea</i>)	<i>Ceramium rubrum</i>
<i>Ralfsia clavata</i> (on shells and small pebbles)	<i>Pterosiphonia fruticulosa</i>
<i>Chondrus crispus</i>	<i>Chylocladia ovata</i>

together with *Cruoriella Dubyi* and *Ralfsia clavata* on small stones. The whole

Sub-littoral association on pebbles and boulders partly covered by sandy-mud (cont.).

RHODOPHYCEAE (cont.)	Barloge W.			Tranabo 24			Southern's Bay			Lough S. 14-17			Cloghan Island			Lough N. 12		
	Sp.	S.	A.	Sp.	S.	A.	Sp.	S.	A.	Sp.	S.	A.	Sp.	S.	A.	Sp.	S.	A.
<i>Chylocladia kaliformis</i>	x	x	.	.	x	.	.	x	.
<i>C. ovata</i>	x	x	.	x	x	x
<i>Nitophyllum punctatum</i>	x	.
<i>Polyneura Gmelini</i>	x	x	.	x	x
<i>P. Hilliae</i>	x	x	.	x	x
<i>Delesseria sanguinea</i>	x	x	x
<i>Membranoptera alata</i>	.	.	.	x	x	x
<i>Hypoglossum Woodwardii</i>	x	x	x	x	.	x	x
<i>Cryptopleura ramosa</i>	.	.	.	x	x	x	x	.	x	x
<i>Laurencia obtusa</i>	x	.	.	x	x	.
<i>L. caespitosa (=hybrida)</i>	x	x	x	.
<i>L. pinnatifida</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Chondria dasyphylla</i>	x	.	.	.	x	.	.	x
<i>Polysiphonia rhunensis (?)</i>	x	.
<i>P. fibrata</i>	x
<i>P. urceolata</i>	x	x
<i>P. violacea</i>	x
<i>P. fibrillosa</i>	x	x
<i>P. variegata</i>	x	.	.	x
<i>P. furcellata</i>	x
<i>P. nigra</i>	x	x
<i>P. nigrescens</i>	x	.	.	x	x	x	x	x	x	.	x	x
<i>P. Brodiaei</i>	.	x
<i>Pterisiphonia parasitica</i>	.	x
<i>P. fruticulosa</i>	.	.	.	x	x	x	x	.	x	x	.	.	x	.
<i>Dasya arbuscula</i>	.	x
<i>Monospora pedicellata</i>	.	x
<i>Rhodochorton floridulum</i>	x	x	x	x	x	x	x	x	x
<i>Callithamnion roseum</i>	x	x	.	x	x
<i>C. Dudresnayi</i>	x
<i>C. corymbosum</i>	x
<i>C. granulatum</i>	.	x
<i>C. tetragonum</i>	x
<i>Plumaria elegans</i>	x	x	.	x	x
<i>Antithamnion cruciatum</i>	x
<i>A. plumula</i>	x	.	.	x	x
<i>Ptilota sericea</i>	.	x
<i>Ceramium arborescens</i>	x	.	.	x	x	.	x	x
<i>C. diaphanum</i>	x	x
<i>C. rubrum</i>	x	x	.	x	x	x	x	x	x	x	x	.
<i>C. flabelligerum</i>	x
<i>C. echinotum</i>	x
<i>C. ciliatum</i>	.	x	x	x
<i>Dumontia filiformis</i>	.	.	.	x	x	x	x	.	x	x
<i>Furcellaria fastigiata</i>	.	.	.	x	x	x
<i>Polyides rotundus</i>	.	.	.	x	x	x	.	.	.	x	x	x
<i>Corallina officinalis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>C. rubens</i>	x	x	x	x

Sp. = Spring species.

S. = Summer species.

A. = Autumn species (very incomplete).

association is very well defined, and with any encroachment of mud is replaced by the *Chorda* and *Zostera* associations.

(c) Pools.

(36) *Sandy-pool vegetation.* Along the ridge which bounds Tranabo area 27 on its south side and also in areas O.-N. in Barloge Creek, there occur a few pools which have a layer of sandy-mud and which support the growth of a few psammophilous species, e.g. *Furcellaria fastigiata*, *Polyides rotundus*, *Gracilaria confervoides*, *Castagnea virescens* and *Punctaria latifolia*.

(3) **Mud subformation.**(a) *Littoral region.*

(37) *Catenella association.* Wherever at a level above L.W.M. a small amount of mud collects, whether in small crevices in the rock surface, between stones composing vertical walls, or on the sides and under surfaces of boulders and flat rocky slabs, *Catenella repens* is fairly certain to be found. Usually it is a pure growth, but in very shaded habitats it may be mixed with *Bostrychia scorpioides*. As the prostrate branches grow they accumulate more mud which they bind together, and often sheets several square feet in area may be found covering the shaded sides of boulders and as a sub-vegetation to *Asco-phylum* or *Fucus spiralis*. While in the main a mid-littoral species, withstanding moderate exposure to air, it may creep up a muddy-rock surface as far as the *Pelvetia* zone, above which it is displaced by other limicolous associations to be considered below. In very deep shade, e.g. caves, its place is usually taken by *Rhodochorton Rothii*, with which it may sometimes form a joint community. It can withstand brackish and even fresh-water conditions, but is then usually invested with Myxophyceae of which the following are the most common:

Aphanothece pallida
Gloeocapsa crepidinum
Chroococcus turgidus
Oscillatoria nigroviridis
Lyngbya aestuarii

Lyngbya semiplena
Calothrix aeruginea
C. confervicola
C. consociata

Calothrix crustacea
C. scopulorum
Microcoleus tenerrimus
Phormidium spp.

and Chlorophyceae such as *Rhizoclonium* and *Urospora* may thread their way through its upright branches. The plant varies greatly in colour depending upon the degree of exposure to light.

(38) *Limicolous association of vertical banks.* In several somewhat scattered areas of the Lough, the littoral region is backed by boulder clay banks, or mud extends downwards over the rock surface. In such situations a number of green and blue-green algae flourish, either in very mixed associations, or in almost pure growths. Although not exhibiting any rigid vertical zonation, the following may be considered the usual sequence beginning at a level above H.W.M.:

(1) *Nostoc Linckia*, forming greyish lumps only covered at exceptionally high tides, often very shrivelled up; usually quite pure, but occasionally mixed with *Rivularia*.

(2) *Gloeocapsa crepidinum*, forming pale grey narrow bands just above H.W.M.

(3) *Rivularia nitida* forming almost black sheets from the base of the *Pelvetia* zone to the highest reaches of the tide. On horizontal or gently sloping mud at H.W.M. it may form extensive colonies, especially along the west shore of the Goleen. *Rivularia nitida* also occurs on vertical banks at much lower levels, where it frequently overgrows the protruding roots of *Phanerogams*.

(4) *Percursaria percura* usually mixed with dwarf *Enteromorpha intestinalis* as a tufted wavy mass at H.W.M. extending to the *Ascophyllum* belt; usually associated with Myxophyceae.

(5) *Enteromorpha intestinalis*, a very dwarf form (especially near fresh-water trickles), which, at lower depths, assumes the more normal form.

(6) *Vaucheria* spp. (usually *V. sphaerospora* and *V. coronata*). These form a belt of very dark green colour and of wide bathymetric range, either starting a sequence above *Enteromorpha torta*, or spreading down to about mid-tide level as a substratum for other species, notably the Myxophyceae; often mixed with *Rhizoclonium*.

(7) *Enteromorpha torta*, either alone or mixed with *Percursaria* in a mid-littoral band, whitish or pale green in colour.

(8) *Rhizoclonium hieroglyphicum*, widely distributed, often forming fleecy sheets, especially where fresh water enters; rarely pure, but mixed with *Chaetomorpha aerea* and *Ulothrix* spp., and with many blue-green species.

(9) *Rhodochorton Rothii*, already referred to, forming deep reddish brown mats in shaded places and on the under-sides of stones partly embedded in the mud.

(10) *Chaetomorpha aerea* occasionally occurring in rope-like strands in the *Pelvetia* or *Fucus spiralis* band, or mixed with *Rhizoclonium*.

(11) *General Myxophyceae*. As on the saltmarsh a large number of Myxophyceae occur on these mud banks, mainly as epiphytes on large algae, but occasionally forming a distinct mixed association of themselves, particularly in the zones nearer to the mid-littoral. More than thirty species are to be found (see Gelatinous Myxophyceae Association of the saltmarsh, p. 118).

Some idea of the complexity of this limicolous association may be gathered from the following description of a felt-like brownish green growth about $\frac{1}{2} \times 1$ in. The growth is dominated by *Rhizoclonium*, whose filaments lie nearer the surface, whilst those of *Vaucheria coronata* are deeply embedded in the mud. Occasional plants of *Bostrychia* and *Catenella* occur, their upright branches breaking through the even felt of *Rhizoclonium*. In patches the growth is deep brown owing to the appearance (at a level below the threads of *Rhizoclonium* and *Vaucheria*) of *Sphacelaria* spp., in the presence of which the colour of the cell sap of *Rhizoclonium* turns brown. Lying over the upper surface of the growth are threads of *Chaetomorpha aerea*, with entangled *Chroococcus turgidus*, *Gloeocapsa crepidinum* and *Aphanophece pallida*. Sometimes above these two layers is a third, spongy and gelatinous in nature, in which *Catenella*, *Enteromorpha torta*, *Calothrix scopulorum*, *Lyngbya aestuarii*, and *Oscillatoria nigroviridis* are to be found.

(b) Sub-littoral region.

(39) *Chorda* association. *Chorda filum* occurs in four main regions in the area: in mid-Barloge Creek, where it spreads along the *Zostera* bed up to the

Rapids; in isolated patches along the east shore of Lough Ine and the south shore of Castle Island; in the Goleen, where it spreads up the west shore, thinning out very quickly beyond the entrance to the Goleen; and on the Tranabo side of the Coosh, where it is associated with *Zostera*, on whose prostrate stems it grows epiphytically. It is essentially a plant of muddy habitats growing either in the mud or attached to tiny embedded pebbles, the least degree of turbulence or a change from a muddy to a rocky substratum causing its disappearance. It is usually fringed by the *Laminaria saccharina* association, and in the Goleen and West Lough Ine it forms part of the *Stilophora-Enteromorpha* association. The associated plants will be dealt with when considering the *Zostera* association. The thalli are often densely clothed with epiphytes of which the following are the most common:

<i>Enteromorpha clathrata</i> var. <i>Linkiana</i>	oc.	<i>Sphacelaria cirrhosa</i>	oc.
<i>Ectocarpus confervoides</i>	oc.	<i>Acrochaetium virgatulum</i>	fr.
<i>Pylaiella littoralis</i>	fr.	<i>Ceramium rubrum</i>	fr.
<i>Scytosiphon lomentarius</i>	oc.	<i>C. strictum</i>	oc.
<i>Litosiphon pusillus</i>	ab.	<i>Chylocladia kaliformis</i>	fr.
<i>Colpomenia sinuosa</i>	r.		

On decaying thalli, a blue-green scum of *Anabaena torulosa* is often found.

(40) *Zostera* association. Apart from some scattered plants along the south of Castle Island there are three main *Zostera* beds: *Zostera marina* on the Barloge and Tranabo side of the Coosh, and *Zostera nana* in the Goleen. The two first are associated with *Chorda* in quiet waters on muddy substrata, while except for entangled *Enteromorpha* and *Chaetomorpha*, the third is a pure association surrounding the saltmarsh at the south end of the Goleen. It is practically free of epiphytic vegetation, though a few small species are found on its blades (see p. 121), though *Zostera marina* from spring until end of summer is densely clothed with encrusting and filamentous species. *Zostera marina*, like *Chorda*, occurs in deeper water and on a more muddy substratum than does *Laminaria saccharina*. *Zostera nana*, in the Goleen, is limited mainly by the vertical banks of the saltmarsh or by the rocks and boulders of the mainland, where Fuci or *Cladophora rupestris* replace it above L.W.M. In the deeper water of the central channel of the Goleen it is gradually invaded by *Enteromorpha clathrata* from the *Stilophora-Enteromorpha* association.

Associated with *Laminaria saccharina* near the Coosh and with *Chorda* and *Zostera* in the same region are a large number of species which are arranged on p. 115 in the form of a comparative list.

(4) Saltmarsh subformation.

The general features of the marsh, which stands on an average about 1 ft. 9 in. above the level of the Zosteretum, have already been described. Although comparatively small in extent, several distinct algal communities occur, but the difficulty of identification of many limicolous species has meant that anything approaching a detailed study has been impossible during a

general survey of all the algal communities of the area. As has already been mentioned, each association requires a period of detailed study in order to evaluate correctly the influences at work determining the occurrence and

	<i>Laminaria saccharina</i>	<i>Chorda</i> and <i>Zostera</i>
<i>Enteromorpha compressa</i>	+	+
<i>E. clathrata</i> var. <i>Linkiana</i>	+	+
<i>E. paradoxa</i>	+	+
<i>E. prolifera</i>	+	-
<i>E. intestinalis</i>	+	+
<i>Ulva latissima</i>	+	+
<i>U. Linza</i>	+	-
<i>Cladophora glaucescens</i>	+	+
<i>C. Hutchinsiae</i>	+	+
<i>C. refracta</i>	-	+
<i>Desmarestia aculeata</i>	+	+
<i>Punctaria latifolia</i>	+	-
<i>Scytosiphon lomentarius</i>	+	+
<i>Asperococcus bullosus</i>	+	+
<i>A. fistulosus</i>	+	+
<i>Ectocarpus distortus</i>	-	+
<i>E. confervoides</i>	+	+
<i>Sphacelaria cirrhosa</i>	+	+
<i>Cladostephus spongiosus</i>	+	-
<i>Stilophora rhizoides</i>	+	+
<i>Spermatocchnus paradoxus</i>	+	+
<i>Mesogloia vermiculata</i>	+	-
<i>Cystoseira granulata</i>	+	-
<i>C. fibrosa</i>	-	+
<i>Gelidium corneum</i>	+	-
<i>G. pusillum</i>	+	-
<i>Chondrus crispus</i>	+	-
<i>Gigartina acicularis</i>	-	+
<i>Phyllophora epiphylla</i>	+	-
<i>P. Brodiaei</i>	+	+
<i>Gymnogongrus norvegicus</i>	-	+
<i>Ahnfeltia plicata</i>	+	+
<i>Cystoclonium purpurascens</i>	+	+
<i>Gracilaria confervoides</i>	+	+
<i>Calliblepharis ciliata</i>	+	-
<i>Rhodymenia Palmetta</i>	+	-
<i>R. palmata</i>	+	+
<i>Cordylecladia erecta</i>	+	-
<i>Chylocladia kaliformis</i>	+	-
<i>C. ovata</i>	+	+
<i>Nitophyllum uncinatum</i>	+	+
<i>Polyneura Hilliae</i>	-	+
<i>Erythroglossum Sandrianum</i>	-	+
<i>Apoglossum ruscifolium</i>	-	+
<i>Membranoptera alata</i>	+	-
<i>Plocamium coccineum</i>	+	-
<i>Laurencia pinnatifida</i>	+	+
<i>Polysiphonia nigra</i>	+	-
<i>P. nigrescens</i>	-	+
<i>P. urceolata</i>	+	-
<i>P. fibrata</i>	+	+
<i>Pterosiphonia thuyoides</i>	-	+
<i>P. fruticulosa</i>	+	+
<i>Plumaria elegans</i>	+	-
<i>Antithamnion plumula</i>	-	+
<i>Rhodochorton floridulum</i>	+	+
<i>Ceramium flabelligerum</i>	+	+
<i>C. rubrum</i>	+	-
<i>Dumontia filiformis</i>	+	+
<i>Polyides rotundus</i>	+	+
<i>Callithamnion roseum</i>	+	+
<i>Porphyra umbilicalis</i>	+	+

distribution of its component species, and there can be little doubt that the three small saltmarshes which occur at Lough Ine would amply repay fuller and consecutive study. The following is a brief descriptive account of the chief algal communities observed (Diatoms omitted).

The phanerogamic vegetation of the island and mainland consists of:

<i>Juncus maritimus</i>	l.dom.	<i>Aster Tripolium</i>	fr.
<i>Armeria maritima</i>	ab.	<i>Carex extensa</i>	oc.
<i>Plantago maritima</i>	ab.	<i>Spergularia media</i>	oc.
<i>Glyceria maritima</i>	ab.	<i>Triglochin maritimum</i>	oc.
<i>Salicornia herbacea</i>	l.ab.		

In addition there are a few local intrusions of *Phragmites vulgaris*, *Suaeda maritima* and *Agrostis alba*. Algae are found colonising the bare mud between the phanerogams, as epiphytes on their rhizomes or exposed roots, in the numerous "pans" which are present, and on the vertical mud banks which arise from the *Zosteretum* or from the rock below.

(41) *The algal association of the pans.* Pans of recent origin, varying in depth from 3 to 10 in., bear a fringe of algal vegetation which spreads out on the surface of the water which they contain. A flocculent growth of inextricably intertwined *Chaetomorpha litorea* and *Cladophora fracta* var. *flavescens* ramifies amongst floating thalli of *Fucus spiralis*, the basal thickened end of whose midrib is embedded in the marginal mud. *Chaetomorpha* and *Cladophora* are attached by a basal cell to the exposed roots and rhizomes of phanerogams, and the three algae may be said to form together a "fringing benthos." The water within the pan supports a plankton in which, in addition to many Diatoms, larval stages of Crustacea, and two species of *Peridinium*, *Chroococcus turgidus* and *Gomphosphaeria aponina* are abundant, especially the latter. The cells of the *Gomphosphaeria* are narrower and longer than those typical of *G. aponina*, and it is probably a distinct saltmarsh variety. At the bottom of many pans is a loose-lying, bluish green community, consisting of an almost pure association of *Gomphosphaeria* with occasional *Chroococcus turgidus*, while on decaying algal thalli, washed up in the Goleen and often deposited at the bottom of the pans, there is often a distinct algal community in which *Anabaena torulosa*, *Calothrix consociata* are prominent, mixed with Bacteria and Protozoa. *Ochlochaete hystrix* was found several times in these decaying masses, together with Diatoms, *Lyngbya semiplena*, *Ulothrix flacca* and *Chroococcus turgidus*.

(42) *Limicolous Fucaceae association.* Conspicuous amongst the phanerogams of the marsh are the limicolous forms of the Fucaceae. The zoning which these exhibit so markedly in the Goleen, the Lough and the Creek is not noticeable on the marsh, so that although there occur small local societies dominated by one or other of the forms, the distribution of both societies and individuals is too irregular to be of ecological significance. It may be well, therefore, to refer to this community as a *Scattered Association of Limicolous Fucaceae*.

There is still much confusion regarding nomenclature of saltmarsh Fuci. Sauvageau up to 1927 has maintained *Fucus lutarius* as a composite species, including therein limicolous forms of *F. platycarpus*, *F. dichotomus*, and possibly *F. vesiculosus*. Chemin (1925) agrees with Baker (1916) in grouping together the saltmarsh Fuci as derivatives of *F. vesiculosus*, but retains the nomenclature suggested by Chauvin in 1831—namely *F. vesiculosus* var. *lutarius*. Baker (1916) and Cotton (1912) recognised that a classification must be based on ecology as well as morphology, and it is upon this that I have based my list, though it is evident that the ecads are connected by many intermediate types, which are to be found on the clay banks that occur sporadically in the Goleen and along the south shore of Lough Ine. The fact that these intermediate forms are so easily found both on the marsh and nearby might be taken as evidence that the ecads suggested by Baker were established on criteria difficult of application, but actual experience in the field, which is perhaps the best test, indicates that the majority of the forms can be grouped without difficulty into the three ecads *volubilis*, *caespitosus* and *muscoides*. When it is recalled that the existing marsh is but a remnant of a much larger one, and that, as in the Lough as a whole, a great deal of telescoping of vegetation has occurred, it is not surprising to find the ecads approximating more closely to each other than they do on the more extensive marshes for which they were first described. The following occur:

(1) *Pelvetia canaliculata* megecad *limicola* ecad *libera*, in scattered patches, branches intertwined, and densely clothed with adventitious branches at the base.

(2) No limicolous forms of *Ascophyllum nodosum* occur, but along the eastern border of the marsh, amongst *Phragmites* and *Juncus*, there are patches of loose-lying *Ascophyllum* washed up and retaining their vitality in regions flooded by the tide.

(3) *Fucus spiralis* var. *nana* occurs together with the normal form on the vertical clay banks of the islands and will be referred to later in connection with the vegetation of these banks.

(4) *Fucus vesiculosus* megecad *limicolus* ecads *volubilis*, *caespitosus* and *muscoides* (ecad *caespitosus* being the most common) forming a close turf overlying the rhizomes of *Armeria*. The densely crowded and very short plants of ecad *muscoides* are mainly in the Juncetum. Although occurring at times in pure local societies, the Fucaceae are usually associated with two other communities: the *Bostrychia-Catenella* association and the gelatinous Myxophyceae association.

(43) *Bostrychia-Catenella* association. *Bostrychia scorpioides* and *Catenella repens* occur as an undergrowth to the phanerogams, especially *Armeria maritima* and *Plantago maritima*, forming a close matted turf. On more extensive marshes this community is of ecological importance in maintaining more

equable moisture and chemical conditions in the soil, but on one so small and so constantly flooded as that at Lough Ine it can hardly be said to have this value. The individual plants rarely possess the deep red colour characteristic of the Rhodophyceae, and the gradation in colour which they exhibit appears to be dependent upon:

- (a) the degree of exposure to light;
- (b) the salt content of the surrounding medium.

In the case of *Catenella* the upright branches, exposed to light and frequently washed by rain water, are greenish in colour; the horizontal branches, protected by the upright ones and in contact with a saline soil solution, are reddish, and become deep red as they penetrate into the soil. Similarly with *Bostrychia*, exposed branches creeping over leaves and rhizomes of Phanerogams are pale red or greenish, whilst those intertwined amongst the horizontal branches of *Catenella* are often a rich red.

The following occur regularly as epiphytes on *Catenella repens*: *Dermocarpa prasina*, *D. incrustans*, *Calothrix confervicola*, *C. aeruginea*, *Ulothrix implexa*, and various Diatoms, germling Fuci and hormogones of *Oscillatoria* and *Phormidium*. *Bostrychia scorpioides* bears the same epiphytes with the addition of *Calothrix fasciculatus* and *Amphithrix violacea*.

(44) *Gelatinous Myxophyceae association*. Often the *Bostrychia-Catenella* turfs are completely covered by the *Gelatinous Myxophyceae community*, which may be described as ubiquitous. It is present on bare soil, on the exposed roots and rhizomes of Phanerogams, on the thalli and in the angles of the branches of marsh Fucaceae, amongst the branches of such creeping plants as *Spergularia media*, spreading along the underside of the leaves of *Plantago maritima*, *Armeria maritima* and *Glyceria maritima*, and surrounding the bases of stems of *Triglochin maritimum*, *Aster Tripolium* and *Juncus maritimus*. As many as thirty species enter into its constitution, but it is throughout dominated by the loose gelatinous colonies of *Aphanothece pallida* and *Gloeocapsa crepidinum*. Through the mass of mucilage which these two species secrete, filamentous algae ramify and colonial forms abound. In the main the community appears as a greyish green scum due to the predominance of the two Myxophyceae mentioned, but bright blue-green spots occur where such algae as *Microcoleus chthonoplastes*, *Calothrix aeruginea*, *Chroococcus turgidus* are locally in abundance.

Eighteen samples of this community were examined and the following list gives an indication of relative frequencies:

Gelatinous Myxophyceae community.

(Frequency reckoned as occurrence in eighteen samples.)

Filamentous Bacteria	5
Diatoms (about 5 sp. <i>Nitzschia</i> and <i>Navicula</i> type)	13
<i>Chroococcus turgidus</i> Næg.	12
<i>Aphanocapsa marina</i> Hansg.	4
<i>Gloeocapsa crepidinum</i> Thur.	15

Gelatinous Myxophyceae community (cont.).

Gomphosphaeria sp.	8
Aphanothece pallida Rebenh.	18
Spirulina subsalsa var. oceanica Gom.	5
Oscillatoria nigroviridis Thur.	6
O. amphibia Ag.	8
O. Corallinae Gom.	4
Oscillatoria sp. (? sancta)	5
Phormidium tenue Gom.	9
P. autumnale Gom.	3
Lyngbya aestuarii Leibm. (mainly vars. limicola Gom. and aeruginea)...	7
L. majuscula Harv.	11
L. semiplena J. Ag.	10
L. Rivulariarum Gom.	4
Microcoleus chthonoplastes Thur.	12
M. tenerimus Gom.	4
Calothrix confervicola Ag.	7
C. consociata Born. et Flah.	4
C. scopulorum Ag.	7
C. crustacea Thur.	3
C. aeruginea Thur.	10
Isactis plana Thur.	2
Rivularia nitida Ag.	5
Nodularia spumigena Mert.	1
Ulothrix implexa Kutz ...	10
Sphacelaria radicans Harv.	2

In addition to the species listed there occur three others:

(1) A species of *Merismopedia*, the cells of which are 1.5–2 μ broad (about one-third the size of those of *M. glauca* Kütz). The colonies are very regular, in the form of rectangular plates of 8–16 cells, and examples occurred in eight of the samples.

(2) A species of *Gonium*—motile colonies of eight cells—arranged rather like those of *G. formosum*, but little more than half their size. This occurred in three samples.

(3) A species of *Calothrix* endophytic in empty sheaths of *Lyngbya aestuarii*.

(45) *Filamentous algae association.* There occur scattered over the marsh small areas devoid of phanerogamic vegetation. They vary in size from less than 1 sq. in., to irregular patches measuring about 15 sq. in., and are colonised by a community of filamentous algae, in the form of flat, flaky sheets, which gradually merge into one of the three previously mentioned communities. In the main these sheets are composed of filamentous green algae such as *Enteromorpha torta*, *Percursaria percura* and *Rhizoclonium hieroglyphicum* agg., together with occasional threads of *Chaetomorpha litorea*, *Ulothrix subflaccida* and *Vaucheria* sp. As usual some Myxophyceae are also present:

Chroococcus turgidus	Gomphosphaeria sp.	Calothrix confervicola
Lyngbya aestuarii	Aphanothece pallida	Microcoleus chthonoplastes
L. semiplena		

In the absence of the larger and more vigorous filamentous greens, like *Enteromorpha* and *Percursaria*, the community tends to become a very mixed one, in which filamentous Myxophyceae predominate and give to the areas

a darker and even blackish appearance in place of the normal pale greyish green. The following algae constitute this type of community:

<i>Oscillatoria nigroviridis</i>	<i>Lyngbya semiplena</i>	<i>Calothrix scopulorum</i>
<i>Phormidium molle</i>	<i>Aphanothece pallida</i>	<i>Anabaena variabilis</i>
<i>Oscillatoria sancta</i>	<i>Microcoleus chthonoplastes</i>	<i>Gloeocapsa crepidinum</i>
<i>Lyngbya aestuarii</i>	<i>Calothrix confervicola</i>	

During dry weather, this community readily flakes off, but the extensive felt-like sheets or rope-like masses of filamentous algae reported from other saltmarshes do not occur at Lough Ine.

(46) *Rivularia* association. Colonies of *Rivularia nitida*, which become confluent as they increase in size, form small local patches on bare soil, but are far less extensive than on clay banks in other parts of the Lough. These *Rivularia* colonies are readily invaded by the Gelatinous Myxophyceae community, and even when this is not the case, filamentous algae such as *Microcoleus* and *Oscillatoria* creep along the hollows and cracks of the colony. Often the *Rivularia* sheet covers a putrefying mass of filamentous algae. The relative rate and extent of development of the filamentous community and that of *Rivularia* appear to depend upon seasonal changes that need to be studied in greater detail.

(47) *Association of vertical banks.* It has already been mentioned that the islands stand at heights varying from 1 ft. 8 in. to 1 ft. 11 in. above the level of the *Zostera* bed. Their clay banks show an interesting and fairly constant zonation.

(1) At the base, passing into the soft mud of the *Zostera* bed, *Vaucheria coronata* spreads as a velvety green covering, thinning out as the banks become steeper and merging into patches of *Rhizoclonium hieroglyphicum*. This zone is much broken up by disintegration of the bank and is absent from some of the islands.

(2) Above the *Vaucheria* zone is a band of *Rhizoclonium hieroglyphicum* mixed with occasional filaments of *Phormidium molle*. *Vaucheria* and *Rhizoclonium* occupy the basal 8–10 in., above which is a broad band consisting of an intimate association of *Phormidium molle* and *Ulothrix implexa*, with a few scattered filaments of *Oscillatoria nigroviridis*. If the bank is overhanging, or if, through erosion, small caves, channels or crevices are formed, the *Oscillatoria-Ulothrix* band is replaced by a *Catenella-Rhodochorton* community—a community characteristic of shaded littoral mud banks in various parts of the Lough.

(3) At the top of the banks, attached to the upper surface of the marsh, but overhanging from 6 in. to 1 ft. may be found a band of *Fucus spiralis*, with occasional plants of var. *nana* on the bank itself, growing in the shelter of the typical form. The plants show a great deal of adventitious branching near the base, and the coiling of the thallus is rather more prominent than is the case with neighbouring saxicolous forms. This coiling is much more in evidence in branches lying flat on the marsh surface or against the clay banks.

A point of interest is the absence of colonies of *Rivularia* which are so conspicuous on clay banks in other parts of the Lough. It would appear that

the constant crumbling away of the banks of the islands makes it impossible for gelatinous colonies to gain a hold, whereas creeping filaments such as those of *Vaucheria*, *Rhizoclonium* and *Ulothrix* are able to establish themselves without great difficulty. These vertical banks, in fact, provide evidence of an interesting conflict between the eroding action of the tide and the work of the filamentous algae whose underground portions bind firmly together the mud particles and possibly add to its quantity from the silt collected by their exposed branches.

(48) *Zostera nana* association. Finally the leaves of *Zostera nana*, which forms an extensive and pure association on the soft mud out of which the eight islands arise, bear an epiphytic and endophytic vegetation which may be treated as a separate algal community. The following species occur:

Aphanothece pallida
Oscillatoria nigroviridis
Lyngbya semiplena
L. aestuarii var. *aeruginea*
Microcoleus tenerrimus, usually associated
 with *Aphanothece pallida*, on and through
 whose gelatinous sheaths it ramifies.
Calothrix aeruginea: often endophytic in de-
 caying cells.
C. consociata: trichomes 22 μ broad.

Rivularia atra: scattered blackish colonies.
Anabaena torulosa: amongst decaying fila-
 mentous algae.
Ectocarpus confervoides
Sphacelaria cirrhosa
Ascoecyclus orbicularis
Enteromorpha clathrata
E. compressa
E. prolifera

The communities described are those which are to be found during July and August. Some of them, e.g. *Bostrychia-Catenella*, the limicolous Fucaceae, and *Rivularia nitida* may be termed perennial, without prejudice to the actual longevity of the individuals comprising them. Other communities are transitory and seasonal. Examination of turfs at other times of the year has revealed seasonal periodicity. In general it would seem that during winter *Vaucheria* and *Rhizoclonium* become relatively more abundant and the Myxophyceae tend to disappear. During early spring *Rhizoclonium* develops rapidly, and along with it species of *Ulothrix* are abundant. In early summer the *Rhizoclonium-Ulothrix* phase is replaced by one in which *Enteromorpha torta* and *Percursaria* are predominant. *Vaucheria*, which seems to be scarce in spring and early summer, begins to develop rapidly in late summer, and its period of activity coincides with the beginning of the Myxophyceae phase which reaches its maximum in early autumn.

It must be remembered that these seasonal changes are at work upon communities much telescoped owing to the small rise and fall of the tide in the Goleen, but growing in certain respects under very favourable conditions.

(1) Owing to the very sheltered conditions which prevail in the Goleen there is little tidal disturbance of the water and consequently very little deposition of silt, except in the Zosteretum. The algal communities are therefore rarely covered by a muddy deposit and their light requirement suffers little interference.

(2) The remoteness of the marsh from the open sea and from the richer algal communities of the Lough, taken in conjunction with the fact that the

prevailing winds drive across rather than down the Goleen, has the effect of reducing greatly the amount of drift or debris which on other marshes often covers extensive patches, causing the algae beneath to die out.

(3) The marsh, including the Juncetum, is flooded for an average of 9 days in each fortnight, and during squally weather the period may be extended owing to the waves breaking over the mud banks during all but neap tides. Except during excessively hot and dry periods, coinciding with neap tides, the moisture and salinity conditions prevailing on the marsh are favourable to algal growth.

It appears to be highly probable that the extensive algal growth thus made possible is of considerable importance in delaying the ultimate break-up of the marsh. Marine algae often act as pioneers on saltmarshes, consolidating the mud particles so that phanerogamic vegetation can develop later on. The algae of the Lough Ine marsh should, however, be looked upon as a rearguard, fighting a gallant but losing battle against the combined forces of subsidence, erosion and denudation. Their allies, the roots and rhizomes of the phanerogams, less well adapted to the task of holding together the soil particles, would allow the retrograde succession to proceed with much greater rapidity were they not aided by the gelatinous sheaths of the filamentous algae ramifying in the soil, often to a depth of several millimetres, and by the consolidating effect of the colonial forms.

(5) Loose-lying community.

Although not occurring so prominently as reported from other countries, a certain amount of vigorous loose-lying vegetation is to be found in quiet waters of the Goleen, and also between the Coosh and Barloge Quay. In the Goleen it consists of a *Monostroma*, which is particularly prominent as a pale green sheet of thalli lying loosely in the mud in spring and early summer. It occurs both in the *Zostera* bed and in the *Stilophora-Enteromorpha* association. It has been quite impossible to identify this species, though it comes fairly near *Monostroma laceratum*. In Barloge Creek the water is sufficiently quiet to allow for normal healthy development of *Laminaria saccharina*, *Cystoclonium purpureum*, and *Ulva latissima*, quite unattached and drifting amongst the fields of *Chorda* and *Zostera*. No conspicuous change of form results from life in this habitat. In the case of *Ulva*, small detached pieces often show considerable new growth, but with *Laminaria* and *Cystoclonium* it appears to be merely a case of prolonged life in spite of detachment.

(6) Algal vegetation of swiftly-flowing water.

Analysis of both the floristic and community aspects of the littoral and sub-littoral regions of the Rapids reveals many striking similarities with the open-coast vegetation. The abundance of richly red algae is in marked contrast to the Lough and to the upper part of the Creek. In the absence of

either deep water or deep shade conditions, their presence must be largely due to the action of swiftly flowing and often turbulent water, which not only creates a well-aerated medium, but a continually changing one of somewhat cooler temperature than that which is found in the Lough and upper Creek. The luxuriance of the Laminarias, and the rehabilitation of *Gigartina*, *Laurencia*, *Ceramium acanthonotum*, *Polysiphonia Brodiaei*, and even of *Porphyra*, in definite belts similar to those which they occupy on the open coast, may be due to a similar set of factors. Amongst the boulders and large stones at the bottom of the Rapids, or as an undergrowth to *Himanthalia* and *Laminaria digitata*, several comparatively rare species such as *Spondylothamnion multifidum*, *Spermatothamnion Turneri*, *Ploeonosporium Borreri*, and *Callithamnion Dudresnayi* occur. A further point of interest is the wealth of *Acrochaetium* spp. which epiphytise the vegetation in the Rapids. Although no special attention was paid to this genus, it is evident that several of these species are new to Britain and possibly to science. A similar remark applies also to species of *Endoderma* and *Erythrotrichia*. There is little doubt that a study of these three genera, which are constantly appearing by chance in ecological collections, would be amply repaid by the wealth of forms and species which occur in the area. The effect of the emergence of this swiftly flowing water into either the Lough above or the Creek below has already been discussed when dealing with the *Cystoseira*, *Laminaria* and *Fucus serratus* distribution in the Lough and that of *Dictyota dichotoma* var. *intricata* and *Saccorhiza* in the Creek.

(7) Fresh-water streams and brackish-water vegetation.

A detailed examination of the narrow stream which enters at the south end of the Goleen revealed a number of interesting points which are here summarised. Beyond the reach of the tides the banks are lined by *Festuca rubra* and *Scirpus*. The first algal communities to appear are local patches of *Vaucheria coronata* and *Ulothrix implexa*, often mixed with the moss *Pottia Heimii*. Later a dark green stratum of *Phormidium molle* with occasional colonies or small sheets of *Gloeocapsa crepidinum* is to be found. Stones and bare stems at the bottom of the stream bear numerous Diatoms and sporeling plants together with two species of *Monostroma*, of which one is *M. Grevillei*. As the stream widens, *Enteromorpha intestinalis* appears and continues to be a prominent feature even beyond the actual estuary, spreading far into the *Zostera* bed beyond. Wherever overhanging grass or mud creates shaded conditions the sheets of *Phormidium molle* appear. *Schizothrix lardacea* and *Rhizoclonium hieroglyphicum* are not infrequent but do not form communities. About 25 yards up the estuary *Fucus ceranoides* appears, at first on muddy banks amongst *Phormidium*, whence it spreads to pebbles and stones in mid-stream. A vertical sequence on the mud at the uppermost reaches of *Fucus ceranoides* reveals (1) from 3 in. below the top of the bank to L.W.M. *Phor-*

midium molle, at first pure, lower down mixed with *Ulothrix*; (2) a dense green plexus about midway down the bank consisting of *Vaucheria coronata* and *Phormidium*; (3) pure *Vaucheria* turf; (4) local patches of *Catenella repens*, associated with threads of *Ulothrix* and *Rhizoclonium*; (5) *Enteromorpha intestinalis* and *Fucus ceranoides* at L.W.M., the latter often covered by blue-green epiphytes belonging to the species already mentioned. An interesting dried up tributary (or possibly a channel worn away by the tide) occurs about 20 yards up the stream. This channel has no fresh water and its algal vegetation is decidedly more marine in character. *Chroococcus turgidus*, *Nostoc Linckia*, *Rivularia nitida*, *Schizothrix lardacea*, *Lyngbya aestuarii* and *Oscillatoria formosa*, with many sporeling masses of *Enteromorpha*, *Monostroma* and *Rhizoclonium* and many plants of *Fucus ceranoides* are found, and a definite zoning of *Rivularia* → *Rhizoclonium* → *Lyngbya* is to be found on the banks and pebbles. Sheets of *Rhizoclonium* are present, as on the saltmarsh, and often conceal other societies beneath them.

Nearing the outlet of the stream the almost vertical muddy banks are colonised by the usual limicolous species, and, as before, *Phormidium molle* forms a dark blue-green carpet, broken in patches by local societies of (1) *Catenella repens* and *Bostrychia scorpioides* in shaded regions; (2) *Enteromorpha torta* dominating a filamentous green association of *Ulothrix*, and *Rhizoclonium*, together with *Nodularia spumigena* and *Spirulina subsalsa*; (3) *Vaucheria coronata*, usually pure; (4) tufts of *Monostroma* sp. fringed by blue-green growths consisting of *Anabaena variabilis*, *Lyngbya Rivularianum*, *Phormidium* sp. and a peculiar marine *Merismopedia* (8-celled). On old shells in the stream bed *Microchaete grisea* occurs. Gradually, near the mouth, the carpet of *Phormidium molle* gives place to sheets of *Rhizoclonium*, often mixed with *Enteromorpha torta*, which overhang in festoons from the projecting top of the bank and cover closely its vertical side. The stream flows out into the Goleen over numerous mud-covered stones which bear copious growths of *Fucus ceranoides* and *Enteromorpha intestinalis*; but the latter, though spreading out over the *Zostera* bed, is replaced by *Chaetomorpha litorea*, which is often in long twisted strands several feet in length. On boulders *Fucus ceranoides* rapidly gives way to *F. vesiculosus*. In other regions the entry of fresh water takes place in small trickles, accompanied by the development of the *Enteromorpha* and *Cladophora* associations already described; whilst at the north-west corner, the volume of fresh water entering is not effective in changing materially the essentially marine vegetation which occupies a pebbly strand, except perhaps in producing an unusually extensive development of ectocarpoid epiphytes on the Fuci.

VI. COMPARISON WITH OTHER AREAS.

Since the publication of Cotton's account of the Marine Algae of Clare Island district no other contribution to our knowledge of their general ecology in the British Isles has appeared, although recently Knight and Parke (37) have dealt with some extremely interesting and important biological problems which have a profound bearing upon marine ecology; and Carter (16, 17, 18) has given an excellent account of the algae of two very distinct types of salt-marsh, whilst Chater (19) has dealt with the conditions prevailing in certain brackish areas in Aberdeenshire. In the Clare Island paper Cotton summarises the main differences between continental algal communities and those occurring in Ireland, and more recent work has not materially affected our conception of the prevailing algal communities of Scandinavia, Denmark, Holland, France and the Mediterranean (see Beauchamp (7, 8), Børge (9), Chemin (21), Du Rietz (29), Funk (29 a), Van Goor (30, 31), Johnson and Skutch (33), Ollivier (41), Printz (42), and Rosenvinge (48, 49)). If a comparison is instituted between the algal communities dealt with in the present paper and those which Cotton enumerates it will be noticed that, although there is a considerable measure of agreement, certain differences exist, and it is to these differences that attention is now drawn.

A. EXPOSED COAST.

There is no *Prasiola* community in the Lough Ine district, though on a visit to Cape Clear Island this alga was noticed on a headland populated by many birds. It is highly probable that it would be found on the Stags and the Kedge.

Enteromorpha intestinalis association. In view of the abundance of *E. minima* on exposed cliffs, and of the presence of other green algae, it seems preferable to revert to Børge's more general term (CHLOROPHYCEAE) though substituting "association" for "formation," especially as it is thus possible to contrast the upper and lower green belts which exist in more sheltered areas.

Bangia-Urospora-Ulothrix association. In the absence of any conspicuous growth of *Ulothrix* on exposed coasts, the latter has been dropped from the title and its occurrence in more sheltered regions, practically pure, has seemed to justify its transference to a separate and distinct community.

Rhodymenia association. Except for a local society in the Rapids, there is no distinct *Rhodymenia* association at Lough Ine. Cotton's suggestion regarding the importance of aspect may account for its absence. It is abundant—in fact dominant—as an epiphyte on *Laminaria Cloustoni*, but does not spread to the littoral region at all.

Callithamnion arbuscula association. The presence of *Ceramium acanthotum* to an equal extent with *Callithamnion* seems to justify a joint title to the association as it occurs on the exposed coasts in this area.

Laurencia-Gigartina association. As will be evident from the description given, the differences in vertical distribution and in horizontal extension which occur between *Laurencia* and *Gigartina* in the Lough Ine district make it necessary to treat each separately. They are quite distinct to the eye and never occur so intimately associated as do, for example, *Bangia* and *Urospora*, or *Callithamnion* and *Ceramium*. Further, the clearly defined limits of *Lomentaria articulata* as a predominantly pendant and sciophilous alga, often occurring independently of either *Laurencia* or *Gigartina*, justify the establishment of a separate *Lomentaria* society. The prevalence of a mid-littoral vegetation, upon a substratum of *Laurencia*, dominated by *Plumaria* and *Ceramium*, is so striking in mid-Barloge, that it has been felt right to treat the association as a distinct unit.

Laminaria association. The possibility of conducting a more detailed study of the exposed sub-littoral region, owing to long periods of calm weather, has led to the inclusion in this association of a distinct *Alaria* BELT, and a separation of a SUB-LITTORAL RHODOPHYCEAE ASSOCIATION which may occur quite independently of *Laminaria*. Further subdivisions of this association were attempted, but owing to the very mixed population it has not been possible to maintain them.

B. SHELTERED COAST.

Porphyra association. As has been indicated, the extension of this exposed community to sheltered regions has not been found at Lough Ine.

Laurencia-Gigartina. Not only is there need to treat these separately on sheltered as much as on exposed coasts, but the constant presence of *Gelidium*, in a similar vertical position has determined the institution of, not only a GELIDIUM ASSOCIATION, but a joint LAURENCIA-GELIDIUM ASSOCIATION, whose composition has been described. In fact, these two latter associations may be said to be amongst the most characteristic of sheltered parts of the Creek. Similarly the continued presence of both a CLADOPHORA RUPESTRIS BELT and of a lower mixed CHLOROPHYCEAE ASSOCIATION have made it necessary to institute additional communities which occupy apparently somewhat similar positions to the *Corallina-Cladostephus* community established by Cotton.

Laminaria association. The peculiar conditions prevailing in the Lough, with the very distinct subdivision of the sub-littoral vegetation, have made it possible to introduce the CYSTOSEIRA and the STILOPHORA-ENTEROMORPHA ASSOCIATIONS in order to give a more complete representation of the algal communities occurring therein.

Sandy-mud rock formation. In the absence of sand unmixed with mud, several of Cotton's communities do not appear at Lough Ine, and the littoral vegetation of the single sandy-mud bay has been treated as one unit. In the sub-littoral region similar associations to the *Pebble-attached*, the *Encrusting*

algae and the *Fruticulose Lithothamnion* associations occur and have been described. In addition, the peculiar conditions prevailing at the base of the Rapids, has led to the description of a *DICTYOTA DICHOTOMA* VAR. *INTRICATA* ASSOCIATION.

Muddy substrata. The very different conditions of the saltmarsh in the Goleen from those described by Cotton for Clare Island, have made it impossible to follow his classification of communities except in outline, but floristically, especially amongst the limicolous Fucaceae, there are many features in common. Finally, a more detailed analysis of the vegetation of mud banks in the Lough and Creek has led to the inclusion of a definite *LIMICOLOUS* ASSOCIATION not treated by Cotton as a separate entity.

As a point of general interest it may be mentioned that the writer, when he first went to Lough Ine, armed himself with a notebook in which were summarised all Cotton's associations, with the idea of just ticking off those which were present. It was the discovery that so few ticks were possible which, during the first few days of the visit in 1930, determined a transference of his attention from the specialised biological problem of epiphytism to the more general problem of attempting to discover the inter-relationships of the algal communities in the area.

VII. THE ALGAL FLORA.

1. MYXOPHYCEAE.

Chroococcus turgidus Näg.
Aphanocapsa marina Hansg.
Gloeocapsa crepidinum Thur.
Aphanothece pallida Rebenh.
Merismopedia glauca Kütz.
Dermocarpa prasina Bornet.
D. incrustans Batt.
Pleurocapsa amethystea Rosenv.
Hyella caespitosa Born. et Flah.
Spirulina major Kütz.
S. subsalsa Oersted
 var. *oceanica* Gom.
Oscillatoria margaritifera Kütz.
O. nigroviridis Thw.
O. amphibia Ag.
O. laetevirens Crn.
O. limosa Ag.
O. sancta Kütz.
Phormidium tenue Gom.
P. molle Gom.
P. autumnale Gom.
Lyngbya aestuarii Leibm.
 f. *limicola*
 f. *aeruginea*
L. majuscula Harv.
L. semiplena J. Ag.
L. lutea Gom.
Symploca hydroides Kütz.
Plectonema tenebrans Born. et Flah.
P. norvegicum Gom.
Mirocoleus chthonoplastes Thur
M. tenerrimus Gom.

Hydrocoleum lyngbyaceum Kütz.
Schizothrix vaginata Gom.
S. lardacea Gom.
Calothrix confervicola Ag.
C. consociata Born. et Flah.
C. scopulorum Ag.
C. Contenarii Born. et Flah.
C. pulvinata Ag.
C. aeruginea Thur.
C. crustacea Thur.
C. fasciculata Harv.
Isactis plana Thur.
Rivularia atra Roth
R. nitida Ag.
R. bullata Berk.
Microchaete grisea Thur.
Nostoc Linckia Born.
Anabaena variabilis Kütz.
A. torulosa Lagerh.
Nodularia spumigena Mert.

2. CHLOROPHYCEAE.

Protococcales.

Chlorochytrium inclusum Kjellm.
Protococcus marinus Kütz.
Characium marinum Kjellm.

Ulvaes.

Protoderma marinum Rko.
Monostroma latissimum Wittr.
M. fuscum Wittr.
M. Grevillei Wittr.
Monostroma spp.
Percursaria percursea Rosenv.

Enteromorpha clathrata J. Ag.
E. clathrata f. *Linkiana* Batt.
 f. *prostrata* Kütz.
E. paradoxa Kütz.
 f. *tenuissima* Kütz.
E. Ralfsii Harv.
E. torta Reinb.
E. prolifera J. Ag.
E. crinita J. Ag.
E. compressa Grev.
E. ramulosa Hook.
E. intestinalis Link.
E. minima Näg.
Ulva lactuca L.
 f. *latissima* DC.
U. Linza J. Ag.

Ulotracheales.

Ulothrix implexa (sub*flaccida* Wille)
U. flacca Thur.
U. speciosa Kütz.

Chaetophorales.

Gloeocystis adnata Näg.
Bolbocoleon piliferum Pringsh.
Endoderma Wittrockii Wille
E. Flustra Batt.
Tellamia contorta Batt.

Cladophoraceae.

Urospora isogona Batt.
Chaetomorpha tortuosa Kütz.
C. litorea Cook
C. linum Kütz.

2. CHLOROPHYCEAE (cont.).

Chaetomorpha aerea Kütz.
C. melagonium Kütz.
Rhizocolonium hieroglyphicum Kütz.
R. riparium Harv.
Cladophora pellucida Kütz.
C. Hutchinsiae Harv.
C. rupestris Kütz.
C. utriculosa Kütz.
C. sericea Kütz.
C. glaucescens Harv.
C. flexuosa Harv.
C. albidia Kütz.
C. Balliana Harv.
C. fracta var. *flavescens* Batt.
C. arcta Kütz.
C. pallida Batt.
C. lanosa Kütz.
Gomontia polyrhiza Born. et Flah.

Siphonales.

Bryopsis plumosa Ag.
Vaucheria Thuretii Woron.
V. sphaerospora Nordst.
V. coronata Nordst.
V. litorea Bang. and Ag.
Codium tomentosum Stackh.

3. PHAEOPHYCEAE.

(Additional to list in previous paper, Rees ((46), pp. 439-442).

Ectocarpaceae.

Microsyphar Polysiphoniae Kck.
Phaeospora brachiata Born.
Stictyosiphon tortilis Rke.
Striaria attenuata Grev.
Streblonema sphaericum Thur.
S. Zanardinii Batt.
Ectocarpus parasiticus Sauv.
E. brevis Sauv.
E. luteolus Sauv.
E. simplex Crn.
E. terminalis Kütz.
E. Holmesii Batt.
E. distortus Carn.
Isthmoploea sphaerophora Kjellm.
Myriotrichia repens Hauck.
Myriactis pulvinata Kütz.
Elachistea Grevillei Arnott.
Leptonema fasciculatum Rke.
Colpomenia sinuosa Derb. et Sol.
Sphaelaria olivacea Pringsh.
Chaetopteris plumosa Kütz.
Stypocaulon scoparium Kütz.
Myrionema Corunnae Sauv.
M. papillosum Sauv.
Ulonema rhizophorum Fosl.
Hecatonema maculans Sauv.
H. speciosum Cotton
H. reptans Sauv.
Ascocyclus foecundus Cotton
Cutleria multifida var. *angustifrons* Holm. et Batt.
Aglaozonia reptans Crn.
Bifurcaria tuberculata Stackh.

Cystoseira fibrosa Ag.
Tilopteris Mortensii Kütz.
Achinetospora pusilla Born.
Taonia atomaria J. Ag.

4. RHODOPHYCEAE.

Bangiales.

Goniotrichium elegans Batt.
Erythrotrichia carnea J. Ag.
E. ciliaris Batt.
E. Boryana Berth.
Bangia fuscopurpurea Lyngb.
Porphyra umbilicalis J. Ag.
 var. *laciniata* J. Ag.
 var. *linearis* Harv.

Nemalionales.

Acrochaetium Chylocladiae Batt.
A. sparsum Batt.
A. Daviesii Näg.
A. virgatum J. Ag.
A. secundatum Näg.
Nemalion multifidum J. Ag.
N. olminthoides Batt.

Gelidiales.

Pterocladia capillacea Born.
Gelidium crinale J. Ag.
G. pusillum Le Jol.
G. aculeatum Batt.
G. pulchellum Kütz.
G. corneum Lam.
G. latifolium Born.

Gigartinales.

Chondrus crispus Stackh.
Gigartina acicularis Lam.
G. stellata Batt.
Phyllophora epiphylla Batt.
P. Brodiaei J. Ag.
P. membranifolia J. Ag.
P. Traillii Holm. et Batt.
Gymnogongrus norvegicus J. Ag.
Ahnfeltia plicata Fries
Actinococcus subcutaneus Rosenv.
A. peltaeformis Schm.
Colacolepis incrustans Schm.
Callophyllis laciniata Kütz.
Callymenia reniformis J. Ag.
Cystoclonium purpureum Batt.
Catenella repens Batt.
Rhodophyllis bifida Kütz.

Rhodymeniales.

Sphaerococcus coronopifolius Grev.
Gracilaria confervoides Grev.
Calliblepharis ciliata Kütz.
C. lanceolata Batt.
Rhodymenia Palmetta Grev.
R. palmata f. *typica* Grev.
 f. *sarminiensis* Grev.
 f. *simplex* J. Ag.
Cordylecladia erecta J. Ag.
Lomentaria articulata Lyngb.
L. clavellosa Gaill.
Champia parvula Harv.
Chylocladia kaliformis Hook.
C. ovata Batt.

Plocanium coccineum Lyngb.
Nitophyllum punctatum Grev.
Myriogramme Bonnemaisonii Kylin

Acrosorium uncinatum Kylin
A. reptans Kylin
Polynaura Gmelini Kylin
P. Hilliae Kylin
P. litteratum Kylin
Cryptopleura ramosa Kylin
 var. *uncinatum* Grev.
Phycodrys rubens Batt.
Delessaria sanguinea Lam.
Membranoptera alata Kylin
Apoglossum ruscifolium Kylin
Hypoglossum Woodwardii Kylin
 var. *angustifolium* Kylin

Rhodomelaceae.

Bostrychia scorpioides Mont.
Rhodomela subfusca Ag.
Laurencia obtusa Lam.
L. hybrida Lenorm.
L. pinnatifida Lam.
Chondria dasyphylla Ag.
Polysiphonia macrocarpa Harv.
P. fibrata Harv.
P. urceolata Grev.
P. elongella Harv.
P. elongata Grev.
P. violacea Grev.
P. fibrillosa Grev.
P. variegata Zan.
P. furcellata Harv.
P. fastigiata Grev.
P. nigra Batt.
P. nigrescens Grev.
P. Brodiaei Grev.
Peterosiphonia complanata Schm.
P. fruticulosa Batt.
P. parasitica Schm.
P. thuyoides Schm.
Brongniartella byssoides Bory.
Dasya arbuscula Ag.
Heterosiphonia plumosa Batt.

Ceramiales.

Spermatothamnion Turneri Aresch.
Ptilothamnion plumula Thur.
P. lucifugum Cotton
Griffithsia corallinoides Batt.
G. flosculosa Batt.
Halurus equisetifolius Kütz.
Monospora pedicellata Sol.
Pleonosporium Borreri Näg.
Rhodochorton Rothii Näg.
R. floridulum Näg.
R. parasitica Batt.
Callithamnion polyspermum Ag.
C. roseum Harv.
C. scopulorum Ag.
C. Hookeri Ag.
C. arbuscula Lyngb.
C. tetragonum Hauck.
C. brachiatum Harv.
C. tetricum Ag.
C. corymbosum Lyngb.

4. RHODOPHYCEAE (cont.).

Callithamnion granulatum Ag.
 Compsothamnion gracillimum Schm.
 Plumaria elegans Schm.
 Ptilota plumosa Ag.
 Antithamnion cruciatum Näg.
 A. plumula Thur.
 var. crispum J. Ag.
 Ceramium gracillimum Harv.
 C. tenuissimum J. Ag.
 C. strictum Harv.
 C. diaphanum Roth.
 C. Deslongschampsii Chauv.
 C. arborescens J. Ag.
 C. botryocarpum Griff.

C. rubrum Ag.
 C. flabelligerum J. Ag.
 C. echinotum J. Ag.
 C. ciliatum Ducluz.
 C. acanthonotum Carm.

Cryptonemiales.

Gloiosiphonia capillaris Carm.
 Grateloupia filicina Ag.
 Dumontia incrassata Lam.
 Dilsea edulis Stackh.
 Schizymenia Dubyi
 Furcellaria fastigiata Lam.
 Polyides rotundus Grov.
 Petrocelis cruenta J. Ag.
 Cruoria pellita Lyngb.

Crouriella Dubyi Schm.
 Peyssonnelia Harveyana Crn.
 Hildenbrandtia prototypus Nardo.
 Schmitziella endophloea Born. et Batt.
 Melobesia farinosa Lam.
 Dermatolithon pustulatum Fosl.
 Lithophyllum incrustans Fosl.
 L. lichenoides Phil.
 Lithothamnion calcareum Aresch.
 L. Lenormandi Fosl.
 L. polymorphum Aresch.
 Epilithon membranaceum Heydr.
 Corallina officinalis L.
 C. squamata Ellis
 C. rubens Ellis et Solan.

VIII. GENERAL PROBLEMS.

EPIPHYTISM AND ALGAL MIGRATION.

The rich epiphytic growth which is to be found on many of the algae in the Lough must undoubtedly affect their distribution. Large species such as *Fucus serratus* and *F. vesiculosus* bearing a heavy weight of epiphytes are more easily torn away during stormy weather, leaving gaps which other species may occupy. The writer is inclined to the view that the very mixed population which is to be found on the mud-covered ledges and boulders and pebbles in Southern's Bay and the south shore of Lough Inc, is in part due to the repeated tearing away of heavily epiphytised algae, allowing the opportunity for any chance spore to develop on the tiny area thus vacated. This tearing away is not simply due to mere weight of epiphytes, but to the fact that the epiphytes capture much of the available light and so cause a light-starvation of the host, which is unhealthily developed and more easily gives way to the strains of wave action. The presence of germling *Alaria esculenta* and *Desmarestia ligulata* amongst the collections brought back from Southern's Bay shows that the spores of these plants drift far up the Creek; while healthy plants of *Polysiphonia Brodiaei* and *Lomentaria clavellosa*, essentially plants of the exposed coasts, have been found near the slip at the top of the Rapids. Except for *Gelidium* and *Corallina*, species with a prostrate thallus are absent from this mixed sub-littoral association, and the erect plants, quickly and heavily epiphytised, have a short existence and give place to others which in turn follow the same course. Even within a period of three weeks during July the vegetation of a single slab will alter materially. A further paper, in course of preparation, will be devoted mainly to the biological relations of epiphyte and host, and the varying degrees of specialisation shown by certain genera, e.g. *Acrochaetium*, *Elachistea* and *Myriotrichia*, etc. From the ecological point of view a further consideration arises, namely, what becomes of the epiphytes during the period when the host plant is either apparently absent, or if the host plant is perennial, how do the seasonal epiphytes spend the inter-seasonal periods? Evidence has been steadily accumulating to show that

there is a good deal of migration of successive generations up and down the shore (see Knight and Parke (37)). This problem of *Algal Migration*, of which the writer has just published a brief account for the Gower coast (44), has not received attention at Lough Ine, but the following observations made during the general ecological survey are of interest.

Dumontia filiformis is a prominent component of the upper sub-littoral and lower littoral flora of the Lough and Creek during spring. By June the plants have almost entirely disappeared, though a few individuals are found in lower regions. There is evidently a downward migration, with diminution in numbers, during summer, followed by an upward migration in spring.

Ceramium acanthonotum. The band of *C. acanthonotum* on the exposed coast is apparently higher during spring than during early and late summer. On an average a rise of 2 ft.-2 ft. 6 in. may occur.

Laurencia caespitosa. In lower Barloge Creek this plant is prominent in the upper *Laurencia* zone during spring. It disappears during summer, a few scattered individuals only being found at L.W.M. as epiphytes on *Gigartina* or *Himanthalia* "buttons." As with the previous two species there appears to be a downward migration during summer, connected, one imagines, with the increased insolation of the summer months, followed by an upward migration in late winter and early spring.

Bangia fuscopurpurea. This alga, which forms such a conspicuous feature of the upper littoral region on exposed coasts during spring, disappears as a distinct community almost entirely during June to August, during which, however, it is found not uncommonly as an epiphyte on *Gigartina*, *Chondrus* and *Cladophora rupestris* near L.W.M. A notable case of upward migration during summer is to be seen in the case of *Enteromorpha clathrata*, which is inconspicuous in spring in the sub-littoral regions of the Lough, but gradually spreads upwards into the mid-littoral region and becomes a conspicuous component of the lower Chlorophyceae association. Similarly *E. compressa*, *E. prolifera* and *Cladophora sericea* are found, as the summer advances, leaving the sub-littoral region and approaching gradually the mid-littoral.

ALGAL PERIODICITY.

The whole problem of seasonal periodicity, intimately bound up with the two preceding phenomena, demands far more exact investigation than has been devoted to it in the past, for the solution of many problems connected with the ecology and distribution of marine algae depends upon a more detailed knowledge of life histories. If Sauvageau's conception of ceaseless activity in the adelophycean stages of certain Phaeophyceae were found to be true also for the Rhodophyceae and Chlorophyceae, it might be found to be the main causal factor in determining the constitution of algal associations at any one time of the year, and would account for the numerous irregularities

in the composition of associations when areas apparently similar, physically, hydrographically and climatically, are compared with each other.

IX. CONCLUSION.

The area investigated provides representative communities of fully exposed, moderately exposed and sheltered coasts, on rocky, sandy-mud covered rock and muddy substrata, together with pools and caves. An analysis of their typical vegetation has resulted in the establishment of several new communities mainly in the region of transition from exposed to sheltered habitats, and in a subdivision of some of the previously recognised associations. While most of the communities are perennial, a few are seasonal, and in view of the fact that so many marine algae are annual, the aspect of the perennial communities is liable to alter considerably as the year advances. In the Lough itself, with its wealth of animal population, especially of the saxicolous type, the influence of biotic factors must be very great, but as yet experimental methods have not yielded satisfactory results (45). The recognition of distinctive communities along the coast is less easy than on land, owing largely to the fact that the requirements of algae are more uniform in character; but their varying ability to resist desiccation, surf-action and insolation, and to adapt themselves to changing conditions of the substratum and angle of slope of the rock, results in the association of species having similar powers of adaptability. Some of these associations are well defined and have clear limits determined by assessable ecological factors; others are ill-defined and more difficult to interpret ecologically. A correct understanding of the causes underlying the distribution of the latter calls for experimental work, not only of an autecological character upon each species involved, but also on a large scale under natural conditions on the sea coast. It appears to the writer that the future of marine algology, as with fresh water algology, must lie mainly in this direction. Nevertheless there is much need for purely descriptive work, for as yet only a few scattered areas of our immense coastline have been investigated.

In conclusion I wish to acknowledge with gratitude a grant from the Royal Society in aid of the expenses involved in this work.

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SEASONAL CHANGES IN VEGETATION IN THE NORTH OF NIGERIA

By P. A. BUXTON.

(*London School of Hygiene and Tropical Medicine.*)

(*With Plates IV—IX and one Figure in the Text.*)

DURING the first half of 1933 I was at Gadau, near Azare, in the north of Nigeria (12° N., 10° E.), studying the ecology of tsetse-flies (*Glossina*). Among other things, photographic records of seasonal changes in the surrounding vegetation were made, and some of these, which are of considerable botanical interest, are reproduced in the accompanying plates. Many of them were taken by my colleague, Mr D. J. Lewis.

The country lies at about 1600–1800 ft. above sea-level: it is nearly flat and undulating and the soil, which is rather sandy, has been thrown up in ridges by the prevailing north-east wind. One could not describe these ridges as dunes, for they are solid and covered with *Combretum* and other small trees: they are evidently of great age, and where they are cut by a road one can see that the deeper layers are consolidated into sandstone. I understand that when wells are sunk, it is found that this sandy soil is of great depth; none of those granite domes and knobs so characteristic of much of the north of Nigeria stand up above the plain in this neighbourhood. Falconer (1911) describes these surface deposits as “alluvium,” without indication of its probable age. The whole area drains towards Lake Chad, and the only considerable river near Gadau is the Katagum River, which only runs for a part of the year.

The climate has been little studied, but resembles that of Kano, which lies 100 miles to the west and at the same altitude. There are two principal seasons: the distribution of pressure, upon which the winds and the climate in general depend, has been recently described by Brooks (1932). During the greater part of the year a dry wind (the harmattan) blows from the north-east: this prevails from October to April, though it is more intense during the middle of that period. This season is rainless, and the humidity is frequently very low. For instance, in March and April the absolute humidity was often 4–5 mm. of mercury. This, combined with the high diurnal temperature, gave relative humidity about 10 per cent. quite frequently. Our lowest relative humidity, 8 per cent., corresponded with dry bulb 36° C., wet bulb 16° C. (2 p.m., March 24th). The month of May is transitional, wind coming up from the south-west and gradually replacing that from the north-east. This is a season of turbulence, thunder and occasional short spells of heavy rain. From

June to September the south-westerly wind is more persistent and the rain steadier. Rainfall records for a period of $3\frac{1}{2}$ years are available from Sherifuri, which lies about 15 miles to the north of Gadau (Lloyd, Johnson and Rawson, 1927): as the altitude and vegetation are similar, these figures are relevant. The annual totals at Sherifuri during that period were from 23 to 36 in., and the mean monthly distribution in the eight rainy months (in inches) was as follows:

March	April	May	June	July	Aug.	Sept.	Oct.
0.07	0.29	2.19	4.02	5.89	12.81	4.29	0.40

At Gadau I have rainfall figures for 1933 only: 42.09 in. fell, half of it in August. The seasonal distribution was much as at Sherifuri, the months January to March and October to December being rainless, and the fall in April only 0.51 in.

As to temperature, we may quote the data from Sherifuri. In $3\frac{1}{2}$ years the lowest temperature of the year always occurred in January, and the absolute minima were 9.4 – 12.2°C . The highest maxima, occurring in April, were 38.3 – 40.0°C . At the onset of the rains, the temperature falls so that in June and the following months maxima of 32.2 – 35.0°C . are expected. From then on to the end of the year, the temperature drops gradually to its minimum in January. From December to February the chill is frequently accentuated by the harmattan, which carries so much dust as to obscure the sun and make large trees invisible at 200 yards.

During our stay at Gadau, we were principally occupied with investigations in the laboratory. But we selected April and July as typical of the dry and of the wet season, respectively. During those two months we made detailed studies of temperature and humidity in Stevenson's screens at an open place outside the laboratory, and also in three places in different types of forest. In each place we exposed maximum and minimum thermometers (N.P.L. Certificates) and thermohygrographs, checked twice daily by whirling hygrometer. Screen 1 was in a sheltered position under a tree on the bank of a small stream, which was completely dry in April but full of water in July. Screen 4 was in a very dense thicket under a large tree swathed in creepers. Both these screens were in "fringing forest" or "river bank association" in the sense defined by Lloyd, Lester, Taylor and Thornehill (1933, p. 234). In contrast with those screens, screen 3 was in open country about 900 yards from the river. It was in an area of "baobab and thorn" of the above authors. Apart from baobab (*Adansonia*), the commonest trees were *Balanites*, *Zizyphus* and occasional *Acacia* spp. The readings obtained in these positions in April (dry) and July (wet) are given in Table I.

The following comments on the table may be made. (1) The range of temperature in all screens is much less in the wet season than the dry: this is due mainly to the fact that the maximum temperatures are lower. (2) The temperature outside the laboratory at Gadau differs very little from that at

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screen 3 in open country; there is also an unexpected resemblance between conditions in those two places and in thicket (screens 1 and 4). It will, however, be observed that the range of temperature in the thickest place of all (screen 4) is considerably less than elsewhere and that this is more evident in the rains than in the dry season. The reason is presumably that in July the thicket is fringed with grass 6 or 8 ft. high and at the same time all the trees are in full leaf. (3) The shade maximum is very important in relation to the biology of *Glossina*, and our readings are discussed fully elsewhere (Buxton and Lewis, 1934). We have tabulated the data to show the number of days in different months on which shade temperature passed 38° C. and also 40° C. for periods of under 1 hour, 1-2 hours, 2-3 hours, etc. There was one day in April when the temperature passed 40° C. in the open for 6 consecutive hours. (4) Soil maxima. Readings were taken at a depth of 1 in. because of their special interest in relation to the pupa of *Glossina*. In Table I we have given the means and the highest and lowest readings in the month from thermometers buried close to each screen. In the paper by myself and Mr Lewis, the data are further analysed and we give the number of days on which the soil maximum was under 40, 40-45 and over 45° C.

Table I. *Temperature records for April and July, outside the laboratory at Gadau, and at three points in or near the permanent home of Glossina. Readings from all places for that period are therefore given for purposes of comparison. The table shows shade maximum and minimum and soil maximum at 1 in., and for each of these the mean (° C. and ° F.), and the highest and lowest readings observed during the period (° C.).*

	Gadau				Screen 3			
	Mean		High ° C.	Low ° C.	Mean		High ° C.	Low ° C.
	° C.	° F.			° C.	° F.		
April 1-30								
Shade max.	39.61	103.30	41.7	35.0	39.95	103.91	42.0	35.0
" min.	23.39	74.10	26.8	17.5	22.95	73.31	26.1	15.6
Soil max.	51.02	123.84	55.4	40.4	51.41	124.54	58.0	41.6
July 1-31								
Shade max.	31.17	88.11	33.6	26.5	30.95	87.71	33.5	26.3
" min.	21.66	70.99	23.9	18.9	21.15	70.07	23.0	19.5
Soil max.	39.22	102.60	46.8	29.4	39.55	103.19	45.6	30.0
	Screen 1				Screen 4*			
	Mean		High ° C.	Low ° C.	Mean		High ° C.	Low ° C.
	° C.	° F.			° C.	° F.		
April 1-30								
Shade max.	38.87	101.97	41.0	34.1	38.64	101.55	40.0	32.8
" min.	20.11	68.20	24.2	13.4	23.66	74.59	27.0	17.4
Soil max.	32.98	91.36	36.2	30.3	29.47	85.05	33.0	28.3
July 1-31								
Shade max.	30.17	86.31	32.5	24.0	29.71	85.48	32.0	25.5
" min.	20.97	69.75	22.9	19.0	23.03	73.45	24.5	21.0
Soil max.	27.76	81.97	31.0	24.4	25.75	78.35	27.2	23.6

* April readings for period 17-30th only.

Every biologist knows that readings of humidity taken at definite hours are of limited value. One wants to know the conditions during the night, and that means that recording instruments must be used. No type of recording instrument is entirely satisfactory, particularly in such a climate as that at Gadau, where the relative humidity may change from 20 to 90 per cent. in a few hours. We employed hair hygrographs which were corrected twice daily by a whirling hygrometer, and we draw the following conclusions from our records.

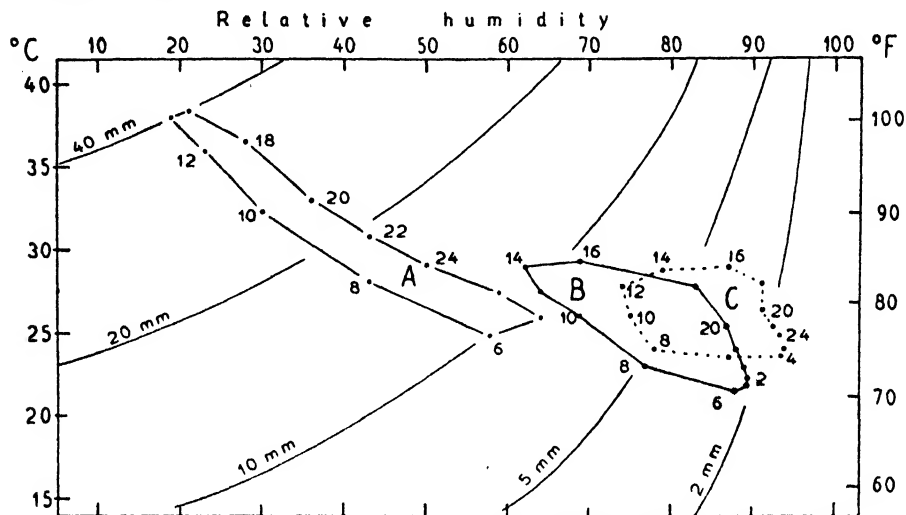
(1) *April*. As a preliminary, the mean relative humidity at 6, 12, 18 and 24¹ hours was worked out for April, for the open exposure at Gadau and the three screens in the country. Even when Gadau was compared with screen 4 (on the ground in dense thicket) the difference was very slight; in general the bush screens were 10 per cent. moister by night, and the differences during the day were slight and irregular. We already know that temperature is nearly the same at Gadau and in the bush during April (Table I); it seems, therefore, that the conditions of temperature and humidity during April show unimportant differences, and it is sufficient at the moment to concentrate attention on the records collected at Gadau. The hygrographs record relative humidity, but we know that saturation deficiency is a more appropriate measurement for biological purposes; in order to convert the readings to that scale, the temperature must be known, and two-hourly means of temperature and relative humidity have therefore been worked out for April at Gadau. For each interval of two hours, the mean of temperature and humidity is spotted on Fig. 1, and when the points are joined they form curve *A*. Lines of equal saturation deficiency are also calculated and added to the graph. It is apparent that the mean conditions by day and by night are very different. Between midnight and dawn (24 to 6 hours), the temperature is a little over 25° C. and the saturation deficiency 10 mm. or slightly higher. From noon till about sunset the mean temperature is over 35° C. and the saturation deficiency approaches 40 mm. The mean of day and night (derived from the two-hourly means) is 31.72° C. with relative humidity 39.5 per cent., i.e. a saturation deficiency of 21.5 mm.

(2) *July*. Two-hourly means of temperature and humidity for Gadau were extracted from the records, and plotted; the result is *B* in Fig. 1. The great contrast between the two months leaps to the eye. In July temperature is lower, and humidity higher; moreover, the difference between day and night is much reduced. If humidity is referred to the saturation deficiency scale, it is seen that at night the deficiency is just over 2 mm. and by day about 10 mm. In fact, if we compare the day in July with the night in April, it is seen that the mean saturation deficiency is the same, and that the difference in temperature is slight. The mean values for the 24 hours are 25.04° C. relative humidity 79.3 per cent., saturation deficiency 4.9 mm.

¹ Times are quoted on this system because it is simpler to show on a graph. Noon is 12, and midnight 24 hours.

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Conditions of temperature and humidity, during July, on the ground in the thicket (screen 4) have been plotted in a similar way, and the result is *C*. The figure shows that the climate here is more damp and more equable than that of Gadau. It seems unnecessary to go to the labour of reducing the data and graphing the temperature and humidity at the other screens, for we already know that conditions at them are intermediate between those in the open plain at Gadau and in the thicket (screen 4). At screen 4 the mean saturation deficiency at night is less than 2 mm. and by day rises to about 7 mm. Combining the two-hourly values, the means for the 24 hours are found to be 25.95° C., relative humidity 86.4 per cent., and saturation deficiency 3.4 mm.



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FIG. 1. Curve *A* gives mean temperature and humidity at two-hourly intervals for Gadau, April 1933. Curve *B*, similar data for Gadau, July. Curve *C*, similar curve for conditions on ground in thicket. The figures are plotted as temperature and relative humidity, but lines of equal saturation deficiency (2, 5 mm. etc.) are shown.

The vegetation of Sherifuri and Gadau has been studied in some detail, particularly in relation to the ecology of tsetse-flies (*Glossina*). For it is well known that the biology of these insects is intimately related to particular types of vegetation, or perhaps to micro-climatic conditions which prevail in thickets, etc. The paper by Lloyd, Lester, Taylor and Thornewill (1933) gives an account of the vegetation, especially of the trees, bushes and grasses, and contains references to earlier work by the same group of investigators. Very briefly, one may say that there are three principal types of vegetation. There are small areas of thicket, some but not all of them on the banks of rivers: some of the trees in these thickets are evergreen, and they are much bound together with creepers. The second type of vegetation is found on open plains liable to flooding: these places are completely bare in the dry season, but



Phot. 3. Plant of *Crinum yuccaeflorum*, photographed five days after the first rain: within that time it has passed from a dry bulb to full flower.



Phot. 2. The same as Phot. 1, photographed on 12th August, nearly three months after the beginning of the rains.



Phot. 1. Part of a large *Ficus*, photographed on 27th March at the end of the dry season.



Phot. 6. The same as Phot. 1, photographed on 12th August; note the still greater development of palm nuts and ground vegetation.



Phot. 5. The same as Phot. 1 photographed on 22nd June; note the development of palm nuts and growth of the ground vegetation.



Phot. 4. Baobab (*Adansonia digitata*) in left background bearing last year's fruits, and large thorny *Zizyphus* in right background. Photographed on 27th March.



Phot. 9. The same as Phot. 7, photographed on 12th August.



Phot. 8. The same as Phot. 7, photographed on 22nd June.



Phot. 7. Largest tree of "African Malogany" (*Kluya* sp.?), photographed on 14th April.



Phot. 11. The same as Phot. 10, photographed
on 12th August.



Phot. 10. Typical "Woodland Savanna," photographed
at the end of March.



Phot. 14. The same as Phot. 12, photographed on 12th August.



Phot. 13. The same as Phot. 12, photographed on 22nd June.



Phot. 12. Photographed on 17th March at the end of the dry season.



Phot. 16. The same as Phot. 15, photographed on 12th August.



Phot. 15. "Woodland Savannah"; photographed on 17th March.

covered with very high grass in the rains. The third type of vegetation, and that which covers much the greatest part of the country, is a thin forest composed mainly of trees of the families Combretaceae and Leguminosae. This thin forest, which is referred to by Lloyd and his collaborators as "woodland savannah," contains a surprising variety of species of tree. I was not in a position to identify them, but I feel certain that there must be at least forty common tree species in the neighbourhood of Gadau. It was extremely interesting to observe the succession of small trees which flowered, even at the height of the dry season. Hardly a week passed without a new one coming into blossom, and this even in places which were far removed from the river. As soon as the rain fell, the transformation was most dramatic. In 1933 the first rain fell in April, but only amounted to 0.51 in. In May there was no rain except between the 16th and 20th, when about 2.0 in. fell. The photograph of *Crinum yuccaeiflorum* Salisb., shown in Plate IV, phot. 3, was taken on May 21st. Five days before, no sign of leaf or flower had been visible. *Pan-cratium* sp. and other bulbous plants burst into leaf and flower with almost equal suddenness. At the height of the rains, in July and October, large areas of the country are covered by flood, so that the conditions of life alter with the season to a surprising extent. The photographs which are reproduced in Plates IV-IX give a clear idea of the seasonal changes in trees, grasses, etc. In particular, it should be noted that in the dry season one can often see for several hundred yards (e.g. Photographs 1, 4, 10, and others): early in the rains the view closes in and at the height of the growing season the grass blots out everything a few yards away (Photographs 2, 14, etc.). The contrast is, of course, much more striking when it is seen in its natural colours in the field. Some of the trees are evergreen (e.g. *Ficus*, Photographs 1 and 2, and *Khaya*, Plate VI), but most are bare in the dry season.

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SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

VI. THE FLORA OF THE SOUTH-EASTERN SLOPES OF MOUNT ELBRUS AND THE UPPER BAKSAN VALLEY, CAUCASUS

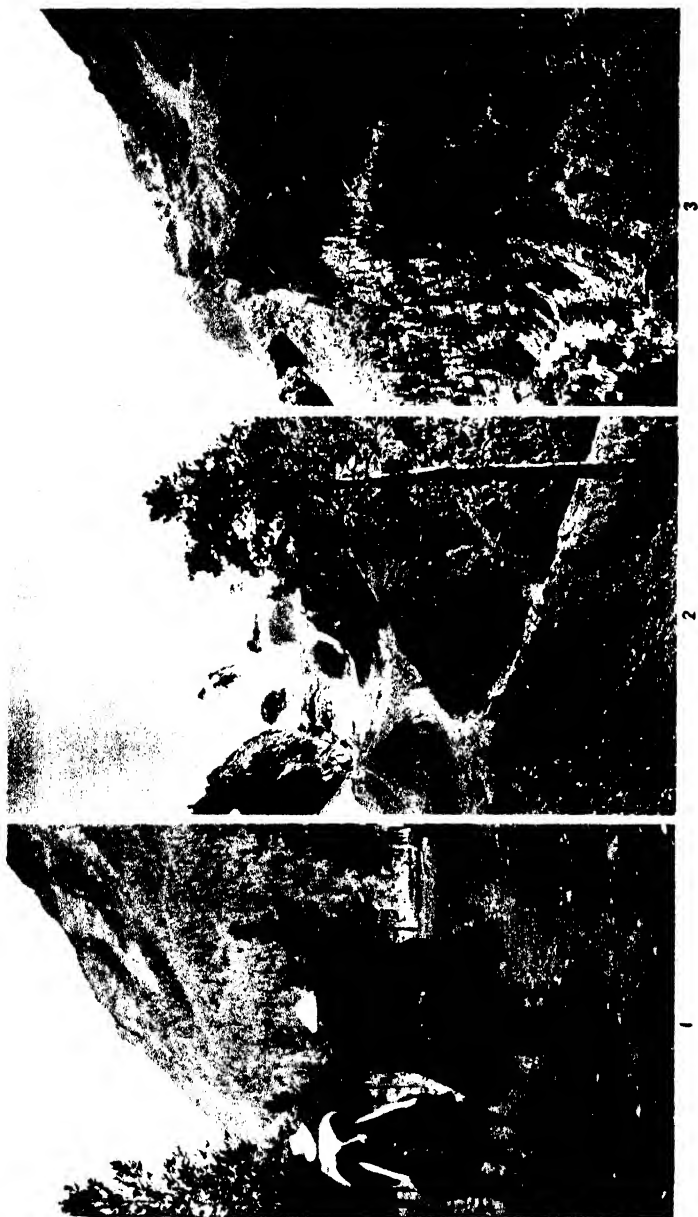
BY WILLIAM SEIFRIZ.

(With Plates X-XII and one Map in the Text.)

THE Caucasus Mountains extend in an easterly-westerly direction from the Black Sea to the Caspian. On the north side, near the western end, is the province of Balkaria. Within Balkaria lie the eastern and south-eastern slopes of Mount Elbrus and the northern slopes of the western half of the main Caucasus Range (Map 1). The largest of the rivers of Balkaria is the Baksan, which has its source in three of the glaciers of Elbrus. Along its upper length the Baksan is fed by a number of tributaries, notably the Irik River on the north, which also springs from Elbrus, and the rivers Dongus-Orun, Uzengi, and Adyl-Su on the south. The last three rise in the main Caucasus Range. It is the plant life of the slopes of these mountains and the valleys of these rivers with which this article deals.

The base from which excursions into this region may be made is Tegenekli, a small native Balkar village, where a house with primitive accommodation is maintained by the Soviet Government. Huts for travellers are now fairly numerous throughout the Caucasus, so that this country, until recently inaccessible and dangerous, has become a safe playground for alpinists and naturalists. Danger from attack is now practically non-existent, the last severe outbreak having occurred four years ago. The greatest problem in planning a journey into the Caucasus at present is food, most of which must be taken along, as even such larger towns as the tourist resort of Nalchik, 130 km. from Tegenekli, have little to offer beyond daily meals. At the alpine bases plain meals and a limited food supply for trips into the mountains are to be had if one possesses a Government food card, an almost indispensable necessity when off the beaten track in present-day Russia.

Tegenekli is situated on the Baksan River south-east of Mount Elbrus (Map 1). It rests at the foot of Elbrus at an altitude of 1780 m. (5785 ft.). The mountains immediately surrounding Tegenekli are very precipitous and rise to maximum heights of 2700-3500 m. Few are snow capped. Behind those on the south side of the valley are the peaks of the main Caucasus Range. At the head of the valley to the west rises Elbrus, with its two peaks of 5631 m. (18,470 ft.) and 5594 m. (18,347 ft.), the highest in Europe. Ad-



Phot. 1. Pine on the slopes of the Upper Baksan Valley.

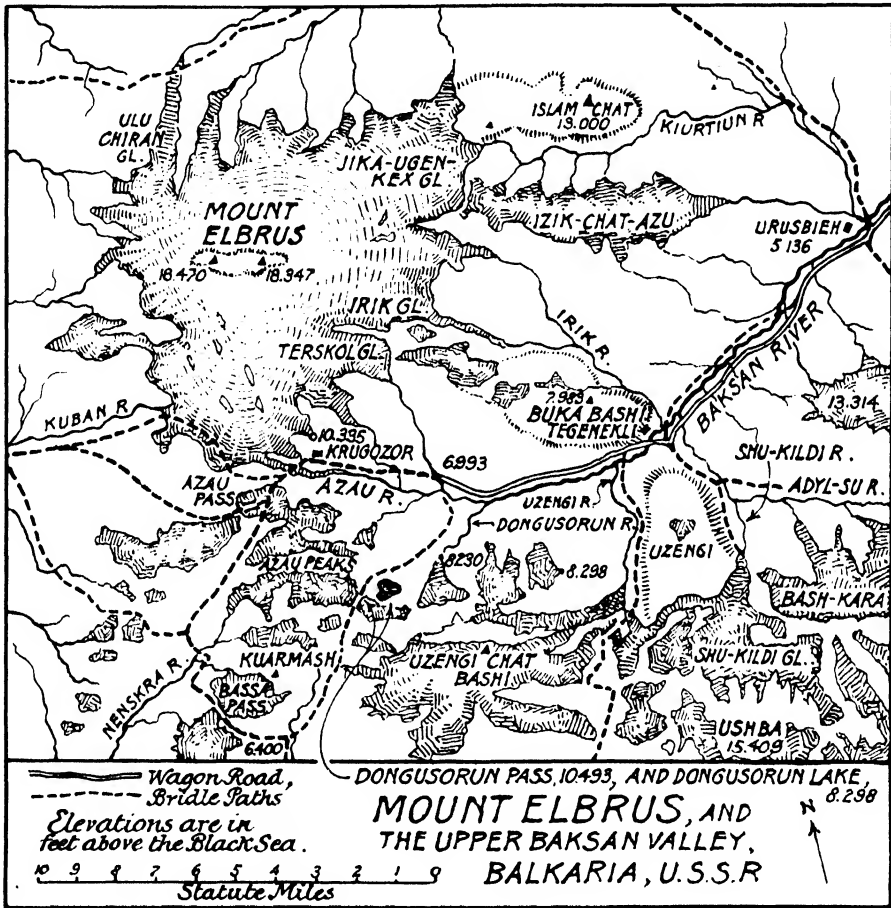
Phot. 2. Looking towards the Shu-Kildi from the Adyl-Su.

Phot. 3. Tree-line of birch with alpine fields above, in the valley of the Adyl-Su.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. VI. FLORA OF SOUTH-EASTERN SLOPES OF MT ELBRUS AND UPPER BAKSAN VALLEY, CAUCASUS

joining Elbrus on the south are the three Azau peaks. The Dongus-Orun (4452 m.) comes next, and then the high peaks of the main range to the south-east.

The northern slopes, that is to say, the slopes with northern exposure, which form the valley of the upper Baksan, are heavily wooded with an almost pure stand of *Pinus hamata*, a variety of the European pine, *P. silvestris*



MAP 1.

(Pl. X, phot. 1). Whether or not this pine is to go under the name of *P. hamata* need not be gone into here, as the question has already been discussed in detail in a former article (1). Bush has suggested the name *P. caucasica* for the Caucasian pine.

The south-facing slopes of the mountains on the opposite side of the valley are almost devoid of trees (Pl. XI, phot. 1), though they contain some pine. They are covered with an herbaceous growth among which two low woody forms are abundant, a *Berberis* and a prostrate juniper.

None of the common deciduous lowland trees, such as *Fagus orientalis*, *Fraxinus excelsior*, *Carpinus betulus*, *Acer campestre*, *A. trautvetteri*, *Prunus avium*, and *Ostrya carpinifolia* occur in the Baksan Valley. The altitude is apparently a little too high for them, although *Acer trautvetteri* goes to 2000 m. in the Minor Caucasus. The most surprising omissions are the spruce and the aspen. When one recalls the fine specimens of *Picea orientalis* in the Minor Caucasus (2), and the relics of former forests of *Populus tremula* at Kasbek (1) in the North-east Caucasus, and further considers, as we shall do later, the abundance of both of these trees in Svanetia just over the mountain tops from Tegenekli to the south, their absence here on Elbrus and the northern slopes of the western end of the main range is difficult to understand.

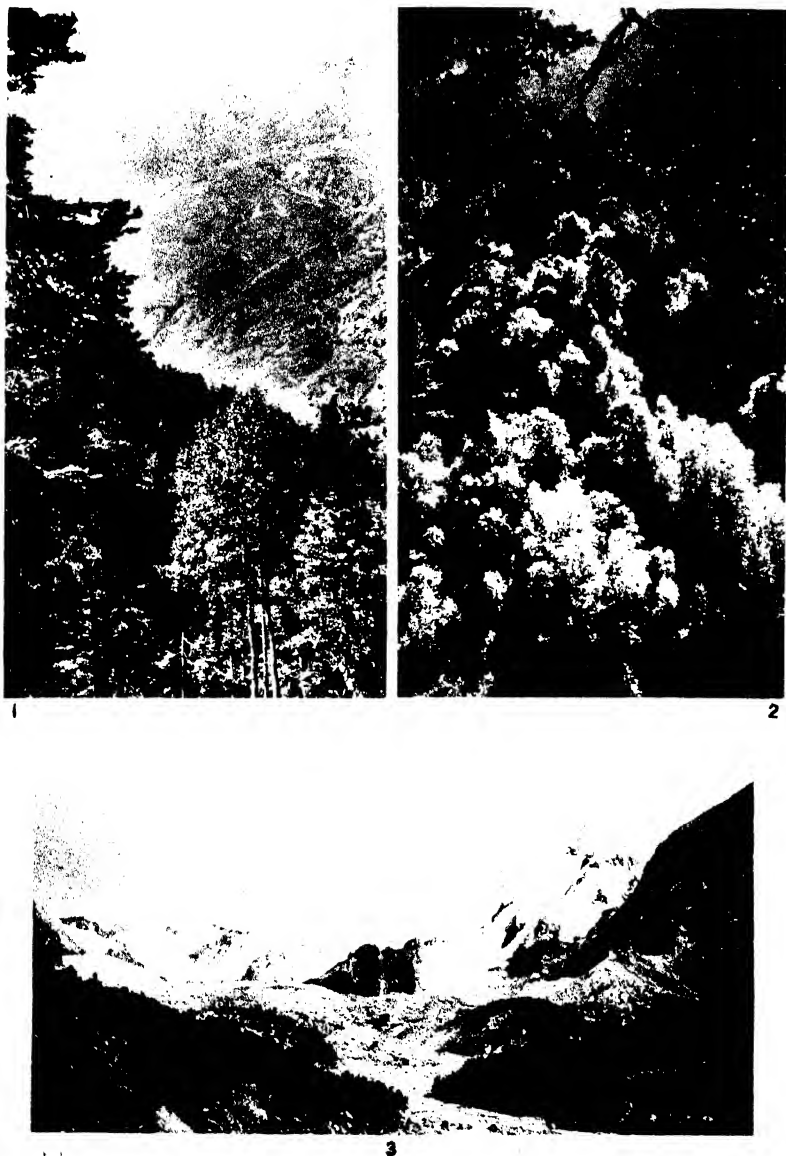
Another conspicuous ecological problem of the upper Baksan and its tributaries is the distribution of the pine and birch. In general, the pine is found in the Caucasus on slopes facing south. This is true of the Baksan Valley and its tributaries only in so far that what trees there are on the south-facing slopes are pine; but these slopes are sparsely covered, and pine is more abundant on the north-facing slopes (Pl. XI, phot. 1) though the birch is abundant here, and predominates at higher altitudes (Pl. XI, phot. 2). The valleys which branch off to the south from the Baksan, those of the three rivers, Dongus-Orun, Uzengi, and Adyl-Su, seem to confuse still more the situation in regard to the distribution of pine; but when the direction of the valleys is noted—the Uzengi to the south, the Adyl-Su to the south-east, and the Dongus-Orun to the south-west—and it is further remembered that southerliness and northerliness, not easterliness and westerliness, determine distribution, then it is found that the flora of these valleys fits into the general scheme. But there are more difficulties elsewhere in Russia; thus, in Svanetia, just over the main Caucasus range from Balkaria, in a country where vegetation is prolific and where the fir, *Abies nordmanniana*, grows excellently, there is little pine. If we summarise the distribution of the pine in Russia, from observations made beyond the Arctic Circle (3), here in the North Caucasus, in Svanetia¹, and in the Minor Caucasus (2), we obtain the following facts:

Kola Peninsula (Arctic region): pine is on dry, sandy, or rocky soil; spruce, its chief competitor, is on clay or wet sand. Determining factors, other than soil, are: the fire hazard, from which spruce suffers most; low temperature, which pine seedlings resist better; root systems, which in the pine go deeper; and vigour, spruce being the more vigorous.

Balkaria (North Caucasus): pine is on south-facing slopes with no competition, dryness being the determining factor.

Svanetia (south side of the main range): there is very little pine, as competition is great, owing to abundant moisture on all slopes; the chief competitors are fir and poplar, both of wide distribution.

¹ "The plant life of Svanetia, Trans-Caucasus" (to follow this article).



Phot. 1. North-facing (left) and south-facing (right) slopes of the Upper Baksan; the former heavily forested with pine and birch; the latter almost barren, a few small pine, some *Berberis*, and prostrate juniper.

Phot. 2. A pure stand of birch in the Uzengi Valley.

Phot. 3. Tree-line of birch on the moraines of the Bash-Kara of the Main Caucasus Range in the Valley of the Adyl-Su.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. VI. FLORA OF SOUTH-EASTERN SLOPES OF MT ELBRUS AND UPPER BAKSAN VALLEY, CAUCASUS

Bakuriani (South Caucasus): pine is on the south-facing slopes, where it is abundant at low altitudes and the sole tree at high altitudes, due to its ability to withstand dryness and low temperatures, and its preference for light.

Armenia (farther south): pine is on the north-facing slopes because the south slopes are too dry for any tree, and the north ones have just sufficient moisture for pine, with very little competition.

The situation in Armenia, where the pine occurs on north-facing slopes contrary to the rest of the Caucasus, resulted in an amusing and heated controversy between the foresters of the two regions, when the question of reforestation arose. Naturally, each group of foresters held out for its respective pine-covered slopes, north in Armenia and south in the Minor Caucasus (Borchom and Bakuriani). The minimum annual precipitation necessary for pine is about 350 mm., that for most other trees is over 500 mm. The former value is the yearly rainfall on the southern slopes of the Minor Caucasus where pine, having no competition, grows to the almost complete exclusion of other trees. The northern slopes receive 700 mm. and harbour a rich mixed forest. The Armenian mountains, on the other hand, have an annual precipitation of 250 mm. on the southern side and 500 mm. on the northern. The former is too little for any form of arboreal vegetation. Grass, therefore, covers the southern slopes. The 500 mm. on the north side is sufficient for pine but barely enough for other trees. As a result, pine is on the north slope in the Armenian mountains and on the south slope in the Minor Caucasus.

Smaller arboreal forms in the upper Baksan are *Prunus*, *Salix*, *Sorbus aucuparia*, and a prostrate juniper. *Sorbus*, so typical of Russian mountains, is but poorly represented in the Upper Baksan. The shrubs have their chief member in *Berberis* which is very abundant on the open southern slopes. In the lower pine forests of the secondary valleys, the typical North Caucasian member of the Elaeagnaceae, *Hippophaë rhamnoides*, grows well.

The plants on the forest floor at 1800 m. are those characteristic of north temperate evergreen forests. The small woody shrubs *Rubus saxatilis*, *Vaccinium vitis idaea*, *V. uliginosum*, and *Empetrum nigrum* are abundant, with an occasional *Rosa*. The more moist localities support several species of *Pirola*, including *P. uniflora* and *P. secunda*.

Sub-alpine life starts at about 1800 m., the altitude of Tegenekli. The roadside herbs here are a mixture of lowland and sub-alpine forms. The following were collected in the neighbourhood of Tegenekli¹:

<i>Lichens</i>	<i>Physcia pulverulenta</i>	<i>C. pyxidata neglecta</i>
<i>Ochrolechia parella</i>	<i>Parmelia bitteriana</i>	<i>Lecanora cinerea</i>
<i>Usnea cavernosa</i>	<i>P. vittata</i>	<i>L. cartilaginea</i>
<i>Alectoria chalybeiformis</i>	<i>Cladonia silvatica</i>	<i>Peltigera canina</i>

¹ I was assisted in the identification of the higher plants by a number of Russian taxonomists of Leningrad. The mosses were identified by Mr R. S. Williams and the lichens by the late Prof. C. C. Plitt. My thanks are due to all for their courtesy.

Bryophytes.

Porella platyphyllum
Pleurozium schreberi
Dicranum strictum
D. scoparium
Dicranoweisia crispula
Tortula ruralis
Tortella tortuosa
Didymodon rubellus
Grimmia ovalis
G. apocarpa
Encalypta ciliata
Funaria hygrometrica
Bryum capillare
Wobera cruda
Polytrichum juniperinum
Hedwigia albicans
Rhytidium rugosum
Hylocomium proliferum
Drepanocladus uncinatus
Cirriphyllum cirrosum
Camptothecium lutescens

Pteridophytes.

Cystopteris fragilis
Asplenium trichomanes
Dryopteris robertiana
D. linneana
Athyrium filix femina
Polypodium vulgare
Equisetum arvense
Selaginella helvetica

Angiosperms.

Polygonum aviculare
Allium victorialis (A. ursinum)
Platanthera chlorantha
Salix triandra
S. pseudomedemii
S. caprea
Betula raddeana
B. alba (B. pubescens)
Stellaria (Alsine) *media*
Minuartia inamaea
Arenaria rotundifolia
Lychnis alba
Thalictrum foetidum
Aconitum nasutum
Anemone albana var. *violacea*
Berberis sp.
Cardamine uliginosa
Sedum spurium (S. roseum)
Sempervivum pumilum
Saxifraga punctata
S. sibirica
S. cotyledon
Ribes grossularia
Sorbus aucuparia
Rubus idaeus
R. saxatilis
Fragaria vesca
Potentilla pimpinelloides
Rosa sp.
Trifolium strepens
Anthyllis boissieri
Lotus ciliatus
Vicia variabilis (V. angustifolia)

Geranium silvaticum
Oxalis acetosella
Euphorbia sp.
Viola rupestris
V. arvensis
Daphne mezereum
Hippophaë rhamnoides
Carum lomatocarum
Pirola secunda
P. rotundifolia
Vaccinium vitis idaea
Swertia punctata
Echium rubrum
Echinopspermum (Lappula) *patulum*
Thymus sp.
Euphrasia sp.
Melampyrum arvense
Galium verum (G. verosimile)
G. cruciata
Lonicera coerulea
L. caucasica
Valeriana alliariaefolia
Campanula sibirica
Psephellus dealbatus
Tanacetum vulgare
Lagoseris (Pterotheca) *orientalis*
Antennaria dioica
Artemisia vulgaris
Senecio renifolius
Lampsana (Lapsana) *grandiflora*
Crepis sp.
Hieracium sp.
Taraxacum sp.
Sonchus palustris

North of Tegenekli is the mountain spur, Buka-Bashi, rising above the River Irik. It offers a superb vista of the main Caucasus Range. West of Tegenekli is the upper end of the valley of the Baksan (Pl. XII, phot. 1). One branch of the valley leads to Krugozor, a small plateau on the slope of Elbrus (Pl. XII, phot. 2). Both of these regions support an interesting sub-alpine flora. More prolific, however, is the high grass vegetation in the valleys of the Adyl-Su, Uzengi, and Dongus-Orun, valleys of supreme beauty headed by majestic peaks and glaciers. The glaciers descend to 2500 m. (Pl. X, phot. 2) and thus eliminate alpine fields in the valley proper, as these usually do not occur below 2600 m. The subalpine pastures extend from 2250 to 2400 m.; beyond them lie moraines and then ice. In the high grass of these five regions the following subalpine forms were collected:

Cystopteris fragilis
Juniperus communis depressa
Calamagrostis arundinacea
Silene inflata
S. commutata
Aconitum orientale
Allium paniculatum
Bistorta sp.
Rumex sp.
Polygonum alpinum
P. bistorta
Dianthus liboschitzianus
Sempervivum pumilum

Saxifraga scleropodia
S. cartilaginea
Potentilla sp.
Alchemilla rotinervis
Trifolium ambiguum
T. alpestre
Coronilla varia
C. vulgaris
Onobrychis viciaefolia
Astragalus galegiformis
Geranium renardi
Viola lutea
Daphne sp.

Epilobium montanum
Chamaenerion (Epilobium) *angustifolium*
Astrantia helleborifolia
Chaerophyllum aureum
Heracleum sp.
Gentiana caucasica
G. septemfida
Cuscuta sp.
Myosotis alpestris
Aquilegia olympica
Ranunculus oreophilus
Alyssum murale



1



2



3

Phot. 1. The upper end of the Baksan Valley with its river, seen from Krugozor on the side of Mt Elbrus.

Phot. 2. The two domes (18,470 ft. and 18,347 ft.) of Mt Elbrus seen from the Krugozor Plateau with the last area of soil adjoining one of Elbrus' glaciers.

Phot. 3. Mt Dongus-Orun from the Pass of the same name: Balkaria to the north (left), and Svanetia to the south (right).

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. VI. FLORA OF SOUTH-EASTERN SLOPES OF MT ELBRUS AND UPPER BAKSAN VALLEY, CAUCASUS

Face p. 144

Hesperis matronalis
H. uncinata
Sedum sp.
Onosma stellulatum
Betonica grandiflora
Teucrium orientale
Nepeta grandiflora
Origanum vulgare
Rhynocorys orientalis
Voronica gentianoides

Plantago media
Scabiosa caucasica
Cephalaria caucasica
Podanthum campanuloides
Campanula rapunculoides
C. hohenackeri
Linosyris vulgaris
Erigeron pulchellus
E. orientalis

Artemisia sp.
Anthemis rudolphiana
Achillea millefolium
Senecio sp.
Cirsium obvallatum
Jurinea arachnoidea
Centaurea fischeri
Mulgedium albanum
Tragopogon reticulatus

Just before the glaciers are reached in the Adyl-Su Valley, one enters a forest of birch, such as forms the tree-line on most of the nearby mountain slopes. The birch forest extends to the moraines of the glaciers of the Bash-Kara (the peaks of the main range) where it dwindles, ending in small scattered trees (Pl. X, phot. 3; Pl. XI, phot. 3). The glaciers and their moraines thus halt the birch at a relatively low altitude (2300 m.), while on adjacent, non-glaciated slopes, woods of the same kind extend up to 2600 m. Within these high birch forests one finds the last indications of a subalpine flora and the beginnings of an alpine one. *Aconitum* spp. are abundant. Forming a rich growth on the forest floor are *Oxalis* and *Linnaea borealis*. The first rhododendrons make their appearance here, but they, like *Daphne*, are rare in the upper Baksan Valley compared with their abundance elsewhere in the Caucasus (1 and 2). Lichens and mosses are prolific, but ferns are rare; the following were collected:

Cladonia pyxidata neglecta
Parmelia sulcata
Alectoria jubata proluxa
Ochrolechia parella
Physcia aipolia

Usnea sp.
Dicranum scoparium
Hypnum uncinatum
Dicranoweisia crispula

Hylocomium proliferum
H. proliferum var. *alpinum*
Webera nutans
Polypodium vulgare

Krugozor is a small but high (3200 m.) plateau on the south slope of Elbrus. A ten minute walk brings one to the Krugozor Glacier (it adjoins the Azau Glacier). Krugozor is an 18 kilometre journey from Tegenekli, the last three kilometres being a severe two or three hours' climb. The Soviet Government has established a hut here, where fire and bedding are supplied. One may climb higher to the "Tent of Eleven" (4200 m.) situated on a rocky protuberance surrounded by ice, from which point the final climb to the summit of Elbrus is made. All land above Krugozor, with the exception of a few rocky projections, is ice-covered. The small terraces and slopes surrounding the hut harbour an alpine flora represented by the following species:

Botrychium lunaria
Polystichum lonchitis
Dryopteris filix mas
Anthoxanthum odoratum
Avena pratensis
A. versicolor
Festuca ovina
Carex caucasica
Crocus sp.
Gymnadenia conopsea
Salix apoda
Minuartia caucasica
M. verna

Minuartia imbricata
Arenaria lychnidea
Sagina sp.
Silene lychnidea
Sedum tenellum
Saxifraga sibirica
S. moschata
S. exarata
S. cartilaginea kolenatiana
Polygala alpestris
P. anatolica
Empetrum nigrum
Bistorta vivipara

Bistorta carnea
Daphne glacialis
Chamaenerion palustre
C. caucasica
Carum carvi
Rhododendron caucasicum
Vaccinium vitis idaea
Primula ruprechtii
P. farinosa var. *algides*
Gentiana pyrenaica
Pedicularis sp.
Valeriana alpestris
Campanula tridentata

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Aetheopappus pulcherrimus
Gnaphalium supinum
Antennaria dioica
Anthemis iberica
Alchemilla caucasica

Potentilla oweriniana
Trifolium polyphyllum
Astragalus daghestanica
Geranium albanum
Senecio nanus

Senecio primulifolius
Leontodon histilis
Hieracium sp.
Pleuragyne carinthiaca

Astragalus daghestanica is an interesting and newly named species, with 1 cm. long balloon-like fruits.

Fifty metres higher (3250 m.) lies a second small plateau immediately adjoining the Krugozor Glacier and moraine (Pl. XII, phot. 2). This plateau is a typical high altitude tundra. From it were collected the following plants:

Woodsia sp.
Festuca ovina
Bromus sp.
Minuartia oreima
Draba begardes var. *imbricata*
Saxifraga exarata
S. juniperifolia
S. cartilaginea
S. sibirica

S. moschata
S. flagellaris
Potentilla oweriniana
Trifolium polyphyllum
Polygala alpestris
Viola biflora var. *caucasica*
Myosotis sp.
Lamium tomentosum
Ziziphora sp.

Veronica gentianoides
Scabiosa ochroleuca
Campanula saxatilis
C. tridentata
C. saxifraga
Aetheopappus pulcherrimus
Aster alpinus
Taraxacum ceratophorum

Nearby rocks yielded the lichens:

Parmelia pubescens
Gyrophora cylindrica
G. proboscidea
Rhizocarpon geographicum
Lecidea pantherina

The journey to the Dongus-Orun Pass takes one to a maximum altitude of 3180 m. Here plant life is essentially the same as that at Krugozor. The Pass (Pl. XII, phot. 3) is one of several possible routes from Balkaria over the Caucasus Range to Svanetia. Botanically, the route is intensely interesting. One leaves, on the north, a rocky and rugged country with few forests, and enters, on the south, a floristically rich country with magnificent forests.

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SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

VII. THE PLANT LIFE OF SVANETIA, TRANS-CAUCASUS

By WILLIAM SEIFRIZ¹.

(With Plates XIII–XVI and two Maps in the Text.)

THE Trans-Caucasian province of Svanetia, now a political division of the Soviet Republic of Georgia, lies just south of the western portion of the Caucasus Mountains (Map 1). Upper or Free Svanetia follows the River Ingur



MAP 1.

between the central Caucasus Range and the Laila Mountains. Lower or Dadiani's Svanetia, so-called because it was conquered by the Georgian,

¹ The present article is the seventh and last of a series on the plant life of Southern Russia which has appeared in this *Journal*.

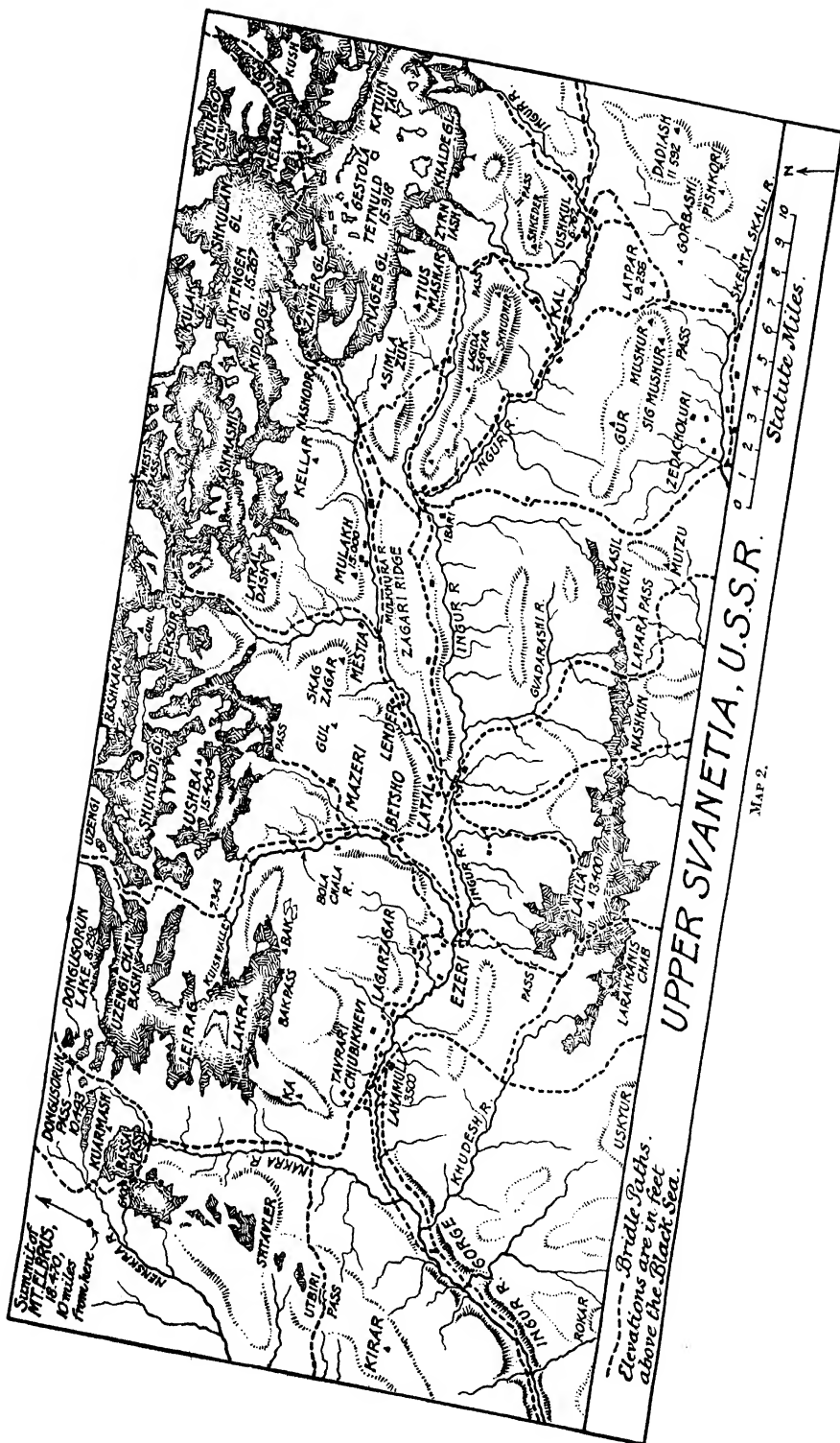
Dadiani, adjoins upper Svanetia on the south, being separated from it by the Laila Mountains. Upper Svanetia is a deep valley 160 km. long and 30 km. wide, with a total area of 3051 sq. km., and a population of 13,000. The natives, like the Balkars of North Caucasus, lead primitive lives, with little culture and no written language, though they are, withal, an interesting and intelligent people.

This article deals with the plant life of Upper Svanetia, from the Dongus-Orun Pass and the Nakra valley at the extreme western end, to the eastern boundary where Svanetia and Ossetia meet (Map 2). The region lies between 43° and 43° 15' N. latitude and 42° 15' and 43° E. longitude.

The first problem which confronts the visitor to Svanetia is that of the route to be taken into the country. Lying in a deep valley, bounded by glaciated peaks on the north and south, and with but slightly less impregnable mountains at its narrow eastern and western ends, Upper Svanetia held back invaders for many centuries. All journeys into and through Svanetia must be made on foot or horseback, as there are no wagon roads. The most used route into the valley is the Latpar Pass at the eastern end, reached from Kutais and Tiflis. Second in importance, and the shortest route, is that entering at the western end, up the valley of the River Ingur from Zugdidi, the terminus of the railroad on the shore of the Black Sea. This way brings one to the small Svanetian village of Lahamuli. Another route, now becoming popular with alpinists, enters Svanetia at its north-west corner, over the Dongus-Orun Pass from Balkaria. This route was followed on the botanical trip here described.

The next problem is that of food. This question will obviously change from year to year during these formative days of the Soviet régime, so that any advice given now may be useless for even the near future. The winter of 1930-1 was one of the most severe in the history of modern Russia. There was a great shortage of food, particularly bread, which, in the Russian mind, is synonymous with food. The Crimea especially, with several other southern provinces, suffered greatly. As a result, travellers, during the summer of 1931, were advised to take along all food necessary when entering Svanetia, but the advice for that year was unnecessary as simple food proved to be reasonably plentiful in the smaller villages, butter, chicken, eggs, mutton, milk, and matzoni or airon (the healthful sour milk of the Caucasus) being usually obtainable, but no bread, except at the tourist bases. The numerous stations established by the Government in the Caucasus serve as places to stop for the night. The accommodation is primitive and the food, when supplied, likely to be rather plain. This is, however, in part compensated for by the natural courtesy of the Russians; they do what they can and give what they have. Simple as is the accommodation, it at least makes possible a journey which, only a few years ago, none but the most courageous dared attempt.

The final problems are luggage and a guide. They are best solved by



purchasing a donkey for the former and dispensing altogether with the latter. One may lose the trail for a time, but the deep valleys clearly indicate the general direction. The native guides are mostly unreliable, especially the Balkars, who are an independent and sullen people. A Balkar guide is likely to be more interested in using his profession as a means to smuggle horses from Balkaria into Svanetia at a profit of 200 roubles, than he is in the welfare of his tourist clients. As a result, he takes the expedition into his own hands, once over the Pass. The Svans, while no more reliable than the Balkars, and less energetic, are a more friendly and courteous people. The killing of a Svan guide by a Balkar, and later retaliation by a Svan, added to the guide problem in 1931. All of these difficulties will diminish as more and more tourists enter Svanetia, and the plans of the Soviet Government to make the country more accessible advance. At present, independent and extensive travel anywhere in Russia requires full equipment from abroad, ample funds, and untold patience.

Any student of the Caucasus should possess that most excellent of all publications on the region by Douglas W. Freshfield (1), if for no other reason than to have the map, which exceeds any other in accuracy and convenience. Unfortunately this superb publication is now to be had only as a rare find.

Entering Svanetia from the north-west, by the Dongus-Orun Pass, has the advantage of affording the opportunity to study first the plant life of the North Caucasus, for comparison with the flora of Svanetia, which is quite different in many respects. The start is made from Tegenekli, which serves as a base for trips into the valley of the upper Baksan River and the southern slopes of Elbrus (described in the sixth article of this series¹). The journey into Svanetia proceeds by foot or horseback up the Dongus-Orun River, a tributary of the Baksan. The valley of the former is one of the most picturesque and botanically interesting regions of Balkaria. A not difficult climb of 15 km. from Tegenekli brings one to the "North Home," which in 1931 consisted of tents only, but they were being replaced by a substantial hut. The night is spent here at an altitude of 2530 m., near the base of the magnificent peaks of the Uzengi Chat Bashi. An early morning start is made in order to reach the glaciers while the snow is still hard. Two hours journeying upward over the glaciers brings one to the summit of the Pass, where the first view into Svanetia is to be had from an altitude of 3180 m. Before one lies the valley of the Nakra River extending directly south (Map 2). The ridge above it on the west marks the western boundary of Svanetia. The landscape of the gorge, the valley of the Nakra, is less severe, more densely forested, and more inviting than the rugged country of Balkaria to the north. No native hut is met until the "village" of Nakra is reached, 20 km. from the Pass. One may spend the night at "Babash," a government-built cabin 15 km. from the Pass (this is the point marked "South Tent" on present government maps), or one may

¹ See pp. 140-146 of this issue.

proceed until sunset and spend the night in the open. The village of Tavrari over the Kva Ridge, can be reached in one day from the Pass, but only with considerable effort.

The valley of the Nakra, through which one journeys from the Dongus-Orun to Tavrari, is one of great interest and beauty. It offers an extraordinary luxuriance of vegetation and a great diversity of species. A more profuse growth of herbaceous plants than that in the high grass region of this valley cannot be imagined. Equally fine is the forest of *Abies* which follows.

The descent from the Dongus-Orun Pass is at first very rapid, over moraine rock, parts of which are covered with ice, thus leaving but few areas where alpine plants could exist. At the Pass, *Minuartia imbricata*, *Myosotis alpestris*, *Saxifraga flagellaris*, *S. exarata*, *S. moschata*, and the moss *Polytrichum piliferum* were collected at an altitude of 3180 m. The rapid descent quickly brings one to a subalpine vegetation.

On the east and west slopes of the Nakra Valley the alpine flora, which tops the subalpine at about 2500 m., is dominated by *Rhododendron*. It grows in great abundance, covering extensive areas. Just below the *Rhododendron*, at 2200 m., are large expanses of the fern, *Athyrium filix femina*. So luxuriant a growth of a single species of fern is seldom to be seen. The presence of such dense stands of fern intermixed with *Rhododendron* is in strong contrast to the complete absence of the latter and the scarcity of the former immediately over the ridge in Balkaria. At a slightly lower altitude, *Athyrium* and *Rhododendron* form an association with birch and willow.

At 2000 m. the high grass association commences and continues down to 1600 m. It consists of a dense growth of herbaceous flowering plants in which the tall *Campanula lactiflora*, with its large, pale blue flower, predominates, although its darker cousin, *Campanula latifolia*, whose deep blue bells may be 5 cm. in length, is almost as abundant, as is also *Inula grandiflora*, with its conspicuous, rich, yellow flowers. A giant Umbellifer of the genus *Heracleum*, constitutes a striking feature of the herbaceous flora; it attains a maximum height of 3 m. Geraniums and Polygonums are profuse. Also abundant are the purple *Centaurea nigrofimbria*, the Boraginaceous *Nonnea intermedia*, *Anemone aurea*, *Pedicularis nordmanniana*, *Draba hispida*, the parasite *Orobanche*, *Ranunculus crassifolius*, *R. oreophilus* and *Rhododendron caucasicum*. The bright orange-coloured *Crocus flavus* is frequently to be seen, more so than in the North Caucasus. The grasses, *Poa longifolia* and *Phleum alpinum*, are the most plentiful of the Gramineae. The absence of *Scabiosa caucasica* here and throughout Svanetia is difficult to understand in view of its abundance on the north slopes of the Main Caucasus Range (2), and in the Minor (South) Caucasus (3).

Before the rich herbaceous growth has wholly disappeared, *Sorbus aucuparia*, a small *Salix*, and a *Betula* begin to make their appearance, forming a

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very typical and widespread association with *Rhododendron* and the fern *Athyrium*, in which also occur:

Aconitum orientale
Cardamine seidlitziana
Alchemilla hirsutiflora

Geranium sp.
Pedicularis atropurpurea
Aster caucasicus

Inula grandiflora
Senecio platyphyllus
Mulgedium abietinum

Where snow has persisted low in the valley, one may see the interesting sight of neighbouring willows in various stages of development, the least advanced having leafless twigs and young catkins on August 22nd (Pl. XIII, phot. 1). The melting snow had uncovered the plants but ten days or two weeks before. The adjoining willows were just leafing out, while those farther back were in full foliage. Growing at the edge of the snow and in full flower was *Primula farinosa*, which probably had not been uncovered more than a week. Thriving under an overhanging shelf of melting snow was the grass *Colpodium caucasicum* (Pl. XIII, phot. 2).

The dwarf 1 m. high willow is the forerunner of the upper small-tree forest of *Salix*, *Sorbus aucuparia*, *Fagus orientalis* and *Acer trautvetteri*, all low tree-shrubs at this altitude (1600 m.).

A hundred metres lower, *Abies nordmanniana* makes its first appearance, though it climbs higher out of the valley on the neighbouring mountain slopes. Soon one is within a superb forest of giant firs which attain a trunk diameter of 2 m. and reach up to 50 m. Here again we have a striking contrast with the North Caucasus, where pine is the sole tree-forming conifer. In addition to fir on the south Caucasian slopes, there is also spruce which is lacking on the north side.

The first native huts in the Nakra Valley are met at the lower edge of the *Abies* forest. The place is named Nakra or Naka. Here agriculture begins. Throughout Svanetia wheat is the chief agricultural product, with millet, potatoes, squash, beans, grapes, hemp (*Cannabis sativa*), oats, and barley completing the list of cultivated plants.

The trail into the valley of the upper Ingur River, that is to say into Svanetia proper, leaves the Nakra shortly before the two rivers join, and then turns east over the Kva Ridge. The first glimpse of Svanetia, with the little village of Tavrari and its lone tower in the foreground, is one long to be remembered. The Valley of the Ingur is of unsurpassed beauty (Pl. XIII, phot. 3). The slopes are covered with fir and spruce. The intervening hills are forested mostly with deciduous trees of the genera *Fagus*, *Quercus*, *Tilia*, and, lower, *Juglans*. Among them are specimens of *Ilex aquifolium*, and *Prunus laurocerasus*. The tree-shrub *Corylus avellana* is also abundant, and at a higher altitude *Betula* and *Sorbus* occur. The small fern *Asplenium septentrionale* was collected en route.

The presence of *Juglans regia* and *Vitis vinifera* indicate the mild climate of Svanetia. No exact meteorological data are available, but from the natives the information is gained that the winters in Svanetia are of moderate temperature, and free from severe winds and much snow. My own experience bears



1



2



3

Phot. 1. Dwarf *Salix* in the Nakra Valley, recently (10 days) uncovered from snow; leafless, with catkins on 22nd August.

Phot. 2. The grass *Colpodium caucasicum* growing under a shelf of melting snow in the Nakra Valley.

Phot. 3. Valley of the Ingur, slopes covered with fir and spruce.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. VII. PLANT-LIFE OF SVANETIA, TRANS-Caucasus



Phot. 1. An almost pure stand of *Populus tremula* at Tavrari.

Phot. 2. Approaching Betcho, with Mt Ushba in the left background; slopes covered with *Picea*, *Abies*, *Populus*, *Betula*, *Quercus*, *Acer*, etc.

Phot. 3. *Picea-Abies* forest on the Zagari Ridge, Mestia.

Phot. 4. *Populus-Picea-Abies* association on the Zagari Ridge, Mestia.

witness to an intensely hot midday in August. Precipitation is 600–700 cm. annually. Irrigation is generally practised.

It is at Tavrari that one first realises how conspicuous a feature of the Svanetian forests is *Populus tremula*. It usually occurs scattered among ever-green trees, its tall pale grey trunk and crown of delicate green foliage standing out in strong contrast to the dark colour of the conifers, though it may often form almost pure stands (Pl. XIV, phot. 1).

The night, if not several days, should be spent at Tavrari, food permitting; the Soviet Base, housed in the school, supplies nothing except roof and mattress. One may proceed to the nearby and larger village of Lahamuli, where living conditions are but little better, though the village is very picturesque. The journey of 25 km. from Tavrari to Betcho, easily made in a day, is one of magnificent scenery with *Picea-Abies* forests covering the northern slopes of the Ingur Valley throughout the way.

The large fern *Struthiopteris* with its interesting fruiting frond, later to be met with in abundance, borders the trail to Betcho, with an occasional specimen of *Vincetoxicum officinale*. At Betcho, a stay for the night or longer should be made, if for no other reason than to admire the majestic summit of Mount Ushba (4700 m.), a favourite peak among the natives and visitors, its massive monolith having been ascended but four times (Pl. XIV, phot. 2). The plant life at Betcho is very fine, almost equalling that of the Nakra Valley. The trail continues to Mestia, the capital of Svanetia. It is a village of striking appearance with its many towers (Pl. XV, phot. 1), but it lacks the charm of the smaller villages and suffers from some of the less desirable features of civilisation. It is the starting point for a number of trips of considerable botanical interest.

At Mestia, I had the pleasure of meeting Professor Paul Vinogradoff-Nikitin of the Institute of Forestry at Tiflis, who continued the journey with us. Much of the information given here in regard to the identification, distribution, and ecology of the trees of Svanetia and the Caucasus in general was received from him.

The following is a list of the trees and tree-shrubs of Svanetia. (Synonyms are in parentheses.)

<i>Taxus baccata</i>	<i>Prunus officinalis</i>	<i>Fagus orientalis</i>
<i>Picea orientalis</i>	<i>P. avium</i>	<i>F. orientalis</i> var. <i>microphylla</i>
<i>Abies nordmanniana</i>	<i>P. divaricata</i>	<i>Quercus iberica</i>
<i>Pinus excelsa</i> (<i>P. caucasica</i> , <i>P. hamata</i>)	<i>Ilex aquifolium</i>	<i>Q. pontica</i>
<i>Juniperus oblonga</i> var. <i>reflexa</i>	<i>Acer pseudoplatanus</i>	<i>Q. sessiliflora</i>
<i>J. nana</i>	<i>A. trautvetteri</i>	<i>Rhamnus microcarpa</i>
<i>Tamus communis</i>	<i>A. platanoides</i>	<i>R. frangula</i>
<i>Populus tremula</i>	<i>A. campestre</i>	<i>Tilia caucasica</i>
<i>Salix caprea</i>	<i>A. laetum</i>	<i>Cornus australis</i>
<i>Ulmus elliptica</i>	<i>A. hyrcanum</i>	<i>Rhododendron caucasicum</i>
<i>Berberis integerrima</i>	<i>Juglans regia</i>	<i>R. ponticum</i>
<i>Pirus communis</i>	<i>Corylus avellana</i>	<i>R. flavum</i> (<i>Azalea pontica</i>)
<i>P. malus</i>	<i>Betula pubescens</i> (<i>B. pendula</i>)	<i>Fraxinus excelsior</i>
<i>Sorbus glabra</i>	<i>Alnus barbata</i>	<i>F. oxycarpa</i>
<i>Crataegus</i> sp.	<i>A. incana</i>	<i>Lonicera caprifolium</i>

With few exceptions all of the above plants are to be found in the neighbourhood of Mestia, particularly on the Zagari Ridge (Pl. XIV, phot. 3-4). This latter ridge is an isolated spur lying on the south side of the valley. As one views the ridge at a distance, *Populus tremula* is again the most conspicuous tree.

A close examination of the Zagari Ridge reveals the following details. Dispersed over the lower fields near the village of Mestia, at an average altitude of 1400 m. are wild apple and pear trees, *Pirus malus* and *P. communis*, some of great age. With them is the birch, *Betula pubescens*, which is at its best in the wet canyon of the river. Its pronounced drooping branches have caused it to be distinguished by the name of *B. pendula*. Other woody forms are *Fraxinus excelsior*, *F. oxycarpa*, *Tilia caucasica*, *Salix amygdalena*, *Alnus barbata* (which is replaced at higher altitudes by *A. incana*), *Corylus avellana* (in abundance), *Berberis integerrima* (even more prolific) and *Crataegus* sp. The hawthorns, so numerous throughout the Caucasus, are kept by the Russian botanists within a few species, and not divided into many species as has been done by the American botanists. The small spiny prostrate juniper, *Juniperus oblonga* var. *reflexa* is abundant. A little farther up, growing at the edge of the forest, are two small trees with brilliant red fruits hanging in clusters. One of these is immediately recognised as *Sorbus*, not the familiar *S. aucuparia*, but instead, *S. glabra*; the other is *Viburnum lantana*. *V. opulus* is almost as numerous; the smaller *V. orientale* occurs less often.

The most conspicuous and prolific of the field plants in the fields at the base of the Ridge and around Mestia in general are *Digitalis ferruginea*, and the thorny weed, *Xanthium strumarium*. The disagreeable *Urtica*, *U. dioica* (not the expected *U. urticans*) is present and often infested with *Cuscuta*. An interesting member of the Papilionatae is *Anthyllis vulneraria*; its common name, sandy Trifolium, suggests another genus. *Erigeron acris* is an American weed which found its way into Russia about forty years ago. Other members of the lowland flora are the yellow-flowered *Impatiens nolitangere*, the very small hemi-parasite *Euphrasia officinalis*, a *Euphorbia*, *Verbascum orientale*, *Artemisia absinthium*, *Origanum vulgare*, *Mentha*, *Linaria*, *Plantago saxatilis*, *Achillea millefolium*, *Alcea ficifolia*, *Lotus ciliatus* and a *Chenopodium*.

One does not climb far up the Ridge before meeting the first maples. Three of the six Svanetian species are represented: *Acer campestre* with quite small leaves, *A. trautvetteri*, the most common, with medium leaves, and *A. platanoides*, with very large leaves; the fruits of the species also differ. The small-leaved *A. campestre* is typically a low altitude form, so that its presence in Svanetia at 1400 m. is rather unexpected. *A. platanoides* is the maple of all Europe, and, while characteristically a tree of the lowlands, it is often found at higher altitudes, as here. *A. trautvetteri*, on the other hand, is a high altitude form only. It cannot be made to grow at low altitudes (e.g. in the Tiflis Botanic Gardens).

With the maples in the lower open forests, on the Zagari Ridge, are *Carpinus betulus*, *Prunus avium*, and the two shrubs, *Rhamnus frangula* and *Lonicera caprifolium*.

Before climbing higher to the *Picea-Populus* association, a glance at the deciduous forest floor reveals some interesting small woody forms and herbaceous plants. Very abundant here and throughout Svanetia is *Rhododendron flavum*, a softer-leaved species than its better known relative, *R. caucasicum*. The latter is sharply restricted to alpine regions, but *R. flavum* grows at all altitudes in Svanetia. This species was formerly called *Azalea pontica* and is not to be confused with *R. ponticum*, a low altitude form.

The distribution of these three rhododendrons, *R. caucasicum*, limited to high altitudes, *R. ponticum* to low altitudes, and *R. flavum*, doing well at all altitudes, brings up the usual question of why three such closely related species should show so definite and characteristic a distribution. Temperature, light, moisture, soil, and acidity are possible factors, but Professor Vinogradoff-Nikitin called attention to another factor, brought to light by attempts to grow a mountain rhododendron (named for him) at low altitudes. *R. winogradoff-nikitin* failed to grow in the Tiflis Botanic Gardens after several attempts at transplantation, until someone planted a specimen near the laboratory and watered it with rain water. The plant grew well for several years and then a new caretaker watered the plant by means of the garden hose connected to the usual water supply from the river, and the plant died. Apparently, the rain water was more nearly like the water received by the plant in its natural mountain habitat than was the Tiflis river water. Soil water on mountain tops is practically free of salts. As it seeps through the soil its salt content becomes greater and greater, being obviously greatest at sea level. Rain water would differ little in salt content from the soil water of mountain summits, while the river water of Tiflis possesses a high salt content.

Berries are well represented in the lower open woods of the Zagari Ridge by the two blackberries *Rubus caucasicus* and *R. tenuidentatus*. The former is the usual thorny blackberry, and the latter probably a hybrid (it has glandular hairs, no thorns, and has been introduced for culture). Another berry is the raspberry, *Rubus idaeus*. *R. raddeanus* also occurs. An interesting vine is the large-leaved Dioscoreaceous *Tamus communis*. *Rosa* is represented by a species with huge (3 cm.) fruits; there are fifty species of *Rosa* in the Caucasus.

The white, star-flowered *Parnassia*, which grows throughout the Caucasus and north of the Arctic Circle (4), is a member of the herbaceous undergrowth; others are:

Polygonatum sp.
Paris octopetala
Goodyera repens
Fragaria vesca

Vicia aurantia
Impatiens nolitangere
Lythrum salicaria
Pirola sp.

Gentiana asclepiadea
Swertia punctata
Scutellaria altissima
Digitalis ciliata

The following mosses and ferns were also collected here:

Dicranum scoparium
D. bonjeani

Calliergon turgescens
Webera nutans

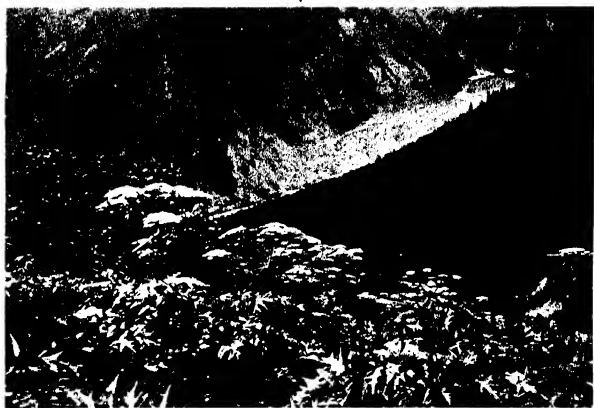
Dryopteris phegopteris

As one climbs upward into the dense forest of large trees, *Picea* and *Abies* begin to make their appearance in substantial form (Pl. XIV, phot. 3). Slightly higher the first large poplars occur, so that at about 1750 m. one finds a well-developed *Picea-Abies-Populus* association (Pl. XIV, phot. 4). The fir does not attain here the huge size that it does in the pure *Abies* forest in the Nakra Valley, but the spruce and poplar do well, the former reaching a maximum diameter of a metre or more and a height of 50 m., while the poplar is almost as large.

Occurring with *Picea*, *Abies*, and *Populus*, and constituting the remainder of the deciduous trees of the association, are *Betula pubescens*, which here rivals the poplar in size and abundance, *Fagus orientalis*, *Quercus iberica*, and *Sorbus glabra*.

The oak ranks third after *Populus* and *Betula* as a prominent member of the deciduous trees of Svanetia. It is widely distributed but stays high, above 1500 m. For those of us who are familiar with the oak in the lowlands of the temperate zone, it is a surprise to find it so far up in the mountains, and never at lower altitudes in the Caucasus. This is, to be sure, also true of the tropics, where, however, the causes are evident; but why the Caucasian oaks are all high altitude forms is less easily explained. Of the four identified Svanetian species, *Quercus iberica* is the most common. The other three are, *Q. pontica*, occurring always above 1800 m., *Q. sessiliflora*, and *Q. hartwissiana* (or *Q. iberica hartwissiana*). Another synonym for the latter is *Q. armeniaca*, though this oak grows in Georgia and not in Armenia. The oak has played an ethnological and nutritive rôle in the history of Russia and Transcaucasia. The fruits of *Q. suber* (*Q. subera*) and *Q. ilex* are edible. At one time the Georgians made flour from acorns, as the Armenians still do. The latter make their bread from a mixture of the flour of sweet acorns and wheat. The language demonstrates the relationship between the oak and food; "Muka" is Georgian for "oak" and Russian for "flour," while "Queri" is Georgian for "dough." (Sanskrit is the origin of the Georgian language as it is of Latin.)

The forest floor at 1750 m. takes on a different aspect and is characterised by *Vaccinium*, of which the small *V. myrtillus* is most common, though the larger *V. arctostaphylos*, the Caucasian blueberry, is more typical of Svanetia. The latter is the largest of the *Vacciniums*, averaging 1 or 2 m. with a maximum of 4 m. and a stem diameter of 8 cm. It is not solely a mountain form, for it grows on the edge of the Black Sea at Batum. Unlike the three other *Vacciniums* it is not found in the north. Formerly, when private trade existed in Russia, *V. arctostaphylos* was a dishonest substitute for tea, not because of similarity in taste, but simply because the leaves of the two look alike, the only difference being a notch in the tip of the leaf of *Thea*, while the *Vaccinium* leaf is pointed.



Phot. 1. Mestia; with *Picea* forests in background.

Phot. 2. The Valley of the Tuibri (at the base of the Latral Dash) near Mestia; *Picea* forest in background; subalpine high grass with specimens of giant *Heracleum* (maximum 10 ft.) in foreground.

Phot. 3. Main Caucasian Range appearing above a forest of *Acer*, *Fagus* and *Quercus*, the last trees before the subalpine fields.

The Zagari Ridge at Mestia is one of the few localities in the Svanetian valley where pine occurs in any abundance. The conifer does not, however, dominate the arboreal vegetation of the Ridge. This honour is held by *Populus tremula*. The scarcity of pine in Svanetia is due to competition, which is especially keen because of heavy precipitation everywhere, as demonstrated by the luxuriance of plant life and the successful agriculture of Svanetia in comparison with the relative barrenness of Balkaria. (Svanetia supplies Balkaria with hay.)

The Latral Dash is an unglaciated peak on the upper Tuibri River at the foot of the Chalaat and Leksur glaciers; it is reached in an easy two-hour walk up the left bank of the Tuibri from Mestia. As it is part of the Main Caucasus Range, it rises to much greater heights than does the Zagari Ridge, which we have just been considering. The slopes of the Latral Dash support a luxuriant high grass association (Pl. XV, phot. 2), above which is an excellent growth of "Krummholz" with alpine fields. *Berberis*, *Crataegus*, *Betula*, *Ilex aquifolium*, and a few scrub pines and spruces constitute most of the bush and small tree vegetation along the river. Before emerging from the low woods the mosses *Dicranoweisia crispula* and *Pogonatum urnigerum* were collected. At 1600 m., near the foot of the glacier where the river has its source, the steep ascent of the Latral Dash begins.

The first plant to greet one in the prolific growth of high grass is *Campanula lactiflora*, 1 m. high, with its large, pale blue flowers. It is exceedingly abundant, as is also a *Papaver* with blossoms of rich orange colour. Higher up, the giant weed *Heracleum* is again met with, standing here fully 2 m. high, with stalks 3-4 cm. in diameter. (There are several mammoth species of this genus, all unidentified.) The following are the plants of the high grass community collected between 1600 and 1800 m. on the slopes of the Latral Dash.

<i>Athyrium filix femina</i>	<i>Alchemilla acutiloba</i>	<i>Heracleum</i> sp.
<i>Aspidium lonchitis</i>	<i>Trifolium ambiguum</i>	<i>Myosotis alpestris</i>
<i>Crocus suwarowianus</i>	<i>Lotus ciliatus</i>	<i>Symphytum asperum</i>
<i>Betula pubescens</i>	<i>Vicia variabilis</i>	<i>Betonica grandiflora</i>
<i>Polygonum alpinum</i>	<i>Lathyrus pratensis</i>	<i>Valeriana alliariaefolia</i>
<i>Silene commutata</i>	<i>Geranium robertianum</i>	<i>Knautia heterotricha</i>
<i>S. compacta</i>	<i>Euphorbia iberica</i>	<i>Campanula lactiflora</i>
<i>Dianthus liboschitzianus</i>	<i>Acer trautvetteri</i>	<i>C. latifolia</i>
<i>Aconitum nasutum</i>	<i>Epilobium montanum</i>	<i>Jasione</i> sp.
<i>Papaver oreophilum</i>	<i>Chamaenerium palustre</i>	<i>Pyrethrum macrophyllum</i>
<i>Sedum involucreatum</i>	<i>Astrantia helleborifolia</i>	<i>Senecio nemorensis</i>
<i>S. maximum</i>	<i>Chaerophyllum aureum</i>	<i>S. platyphyllum</i>
<i>S. pallidum</i>	<i>Monotropa hypopitys</i>	<i>Mulgedium albanum</i>
<i>Aruncus sylvester</i>	<i>Vaccinium vitis idaea</i>	<i>Lapsana grandiflora</i>
<i>Rosa</i> sp.		

At 1700 m. there starts a low, bushy growth of the maple, *Acer trautvetteri*, 2-3 m. tall. Somewhat higher, the maple is replaced by a similar shrubby growth of *Fagus orientalis*. This tree, with its varietal form, *F. microphylla*, grows throughout Svanetia, forming large trees, though here at 1750 m. it is typical "Kniehholz." It often outclimbs all other trees in the Southern Caucasus.

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Above the shrubby *Fagus* are three types of plant communities, low grass, rhododendron thicket, and heath. The first contains typically,

Ranunculus boissieri
Solidago virga aurea
Gentiana asclepiadea

Polygonum bistorta (*Bistorta carnea*)
Hieracium sp.

This small group, with *Geranium* and *Anemone* (*Pulsatilla*) is of wide distribution, occurring throughout the Caucasus, usually intermediate between the high grass (subalpine) and the truly alpine associations. It invariably contains and is usually characterised by the tall pink-flowered *Polygonum bistorta*.

On the edge of this alpine wood of shrubby *Fagus* was a most interesting association of plants that is typical of the far north. Within a foot of each other, on rocky ground, were *Vaccinium vitis idaea*, *Linnaea borealis*, *Empetrum nigrum*, *Goodyera repens* and *Pirola secunda*, plants commonly growing together on the arctic moors at Hibini in latitude 69° (4).

The trail leads on from Mestia to the small villages of Kal and Ushkul, at which point one may turn southward and leave the valley by the high Latpar Pass. Or one may retrace one's steps from Mestia to Lahamuli and leave Svanetia at its western end through the valley of the River Ingur to the south.

The journey from Mestia to Kal is a day's horseback ride and takes one through excellent forests of *Abies*, *Picea*, *Acer* and *Alnus*, with the woodland herb *Gentiana septemfida* abundant along the way. The fern *Struthiopteris* also grows in great profusion. *Sambucus* is met with in the form of *S. nigra*, a small woody tree, later to be replaced by its herbaceous cousin *S. ebulus* in Lower Svanetia. Parasitic on *Abies* is *Viscum album*.

Kal is of no great interest except to serve as a base while making the two and a half hours' journey to Ushkul. This last bit of the Svanetia Valley takes one through an almost pure deciduous forest (Pl. XV, phot. 3) consisting of *Betula pubescens*, *Populus tremula*, *Acer trautvetteri*, *Sorbus*, *Prunus avium*, *P. divaricata*, *Corylus avellana*, *Salix caprea*, *S. pseudomedemii*, *Ribes petraeum*, *Fagus orientalis*, *Quercus iberica hartwissiana* (*Q. armeniaca*), and the woody shrubs *Lonicera xylosteum* and *Viburnum opulus*. The fern *Dryopteris linnaeana* was noticed. No *Abies*, only an occasional *Pinus* and but little *Picea* are here.

Beyond and above the picturesque village of Ushkul lie alpine fields (Pl. XVI, phot. 1) where Rhododendron (*R. caucasicum*) thickets, the small willow, *Salix arbuscula*, and the birch, *Betula pubescens*, crown the hill tops.

The altitude of the village of Ushkul is sufficiently great (2080 m.) for its immediate surroundings to harbour an alpine and subalpine flora, consisting in the main of the following:

Athyrium filix femina
Avena fatua
Calamagrostis arundinacea
Polygonatum polyanthemum
Crocus scharajani var. *flavus*

Betula sp.
Bistorta carnea
Dianthus liboschitzianus
Anemone aurea
Pulsatilla sp.



1



2



3

Phot. 1. The Ushkul Valley.

Phot. 2. *Rhododendron caucasicum* thickets above Kal-Ushkul, approaching the Latpar Pass.

Phot. 3. Alpine fields of *Geranium pasterus* with scattered *Rhododendron* patches near the Latpar Pass, with the greater part of the main Caucasian Range in view; Shkara is on the right, and Tetnuld on the left.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. VII. PLANT-LIFE OF SVANETIA, TRANS-CAUCASUS

<i>Aconitum nasutum</i>	<i>Pedicularis condensata</i>
<i>Sedum</i> sp.	<i>Chamaemelum caucasicum</i>
<i>Saxifraga moschata</i> var. <i>exarata</i>	<i>Scabiosa ochroleuca</i>
<i>Cotoneaster pyracantha</i>	<i>Podanthum campanuloides</i>
<i>Potentilla tormentilla</i>	<i>Campanula collina</i>
<i>Trifolium ambiguum</i>	<i>C. allariaefolia</i>
<i>T. pratense</i>	<i>C. rapunculoides</i>
<i>Geranium sylvaticum</i>	<i>Erigeron pulchellus</i>
<i>Malva neglecta</i>	<i>E. caucasicus</i>
<i>Helianthemum chamaecistus</i>	<i>Solidago virga aurea</i>
<i>Daphne glomerata</i>	<i>Anthemis regiscens</i>
<i>Astrantia helleborifolia</i>	<i>A. rudolphiana</i>
<i>Pimpinella rhodantha</i>	<i>Artemisia</i> sp.
<i>Seseli libanotis</i>	<i>Rhynchocorys orientalis</i>
<i>Vaccinium myrtillus</i>	<i>Senecio nomorensis</i>
<i>Gentiana septemfida</i>	<i>Centaura fischeri</i> var. <i>ochroleuca</i>
<i>G. caucasica</i>	<i>C. nigrofimbria</i>
<i>Betonica grandiflora</i>	<i>Cirsium colchicum</i>
<i>Brunella vulgaris</i>	<i>C. macrocephalum</i>
<i>Veronica gentianoides</i>	<i>Hieracium</i> sp.
<i>Alectorolophus major</i>	

Beyond Ushkul is the superb glaciated ridge of Shkara in the Main Range, and the conical, ice-capped peak of Tetnuld, the "Jungfrau" of the Caucasus.

One returns to Kal for the night, although at Ushkul there is shelter with a caretaker, but without accommodation. From Kal the journey out of Upper Svanetia begins. Happy is the traveller who has good weather, for the trip is one of great splendour. On leaving Kal the trail mounts through a deciduous forest of *Acer trautvetteri*, *Fagus orientalis*, *Quercus hartwissiana* and *Prunus padus*. In these woods the following mosses were collected:

<i>Drepanocladus uncinatus</i>	<i>Pogonatum urnigerum</i>	<i>Polytrichum juniperinum</i>
<i>Pogonatum alpinum</i>	<i>Dicranoweisia crispula</i>	<i>P. alpinum</i>

At the edge of the forest one finds *Colpodium variegatum*, *Alopecurus nagratus*, *Cerastium purpurascens*, *Anemone aurea*, *Inula glandulosa*, and *Daphne mezereum* (with longer and more delicate leaves than *D. glomerata*).

Crocus suwarowianus is first met with on emerging from the forest. It is distinguished from its close relative *Crocus flavus* by its colour, the latter being a rich orange and the former a light yellow. *C. flavus* is abundant in all alpine meadows from Elbrus to the Latpar Pass. *Colchicum autumnale* also occurs.

The approach to the Latpar Pass takes one through extensive alpine fields. No high grass precedes them. On leaving the deciduous forest one soon comes upon large areas of *Rhododendron caucasicum* (Pl. XVI, phot. 2). These continue, alternating with an herbaceous growth in which *Anemone* and *Inula glandulosa* are conspicuous. Shortly before the Pass is reached the last *Rhododendron* patches are left behind and *Geranium pasterus* takes full possession of the fields; its foliage, in autumnal colour of pale rose, tints the mountain slopes for hundreds of metres around (Pl. XVI, phot. 3). The only other plant occurring with *Geranium* in any quantity is a small *Dryas*.

Among the less abundant herbs at the Pass are *Taraxacum*, *Alchemilla sericea*, *Myosotis alpestris* and *Saxifraga sibirica*. The most common grass is

Briza minima. On the rocks within the Pass, the moss *Dicranoweisia crispula* was collected. There is a slight depression in the meadow at the Pass where *Crocus flavus* grows in extraordinary profusion.

The altitude of Latpar Pass is 2835 m. No high mountains lie between it and the Main Caucasus Range, so that one has an unobstructed view from Shkara, the second highest of the Caucasus mountains, on the right (east), to Ushba on the left (Pl. XVI, phot. 3). The panorama is one of unsurpassed beauty, the ruggedness of Shkara's rocky ridge softened by freshly fallen snow, and the white cone of Tetnuld, the most graceful of the Caucasian peaks, glistening in all its splendour. At one's back, to the south, lies the more serene pastoral landscape of Lower Svanetia.

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THE VEGETATION OF AKPATOK ISLAND. PART II

By NICHOLAS POLUNIN.

(*Senior Research Scholar, New College, Oxford: late Henry Fellow at Yale University.*)

(*With Plates XVII—XIX and three Figures in the Text.*)

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HABITATS AND SPECIAL COMMUNITIES (*continued*).

IX. SPECIAL LOCALISED COMMUNITIES.

These are described under a special heading, distinct from "Special localised habitats," to include the many relatively luxuriant or closed (but floristically different) communities whose vegetation is less obviously dependent on some peculiar master factor such as the proximity of nesting birds or the local preponderance of an acid-weathering morainic deposit. Indeed the main factors allowing this local development of a peculiar community were often obscure, especially where the community covered a considerable area. Sometimes

there appeared to be greater stability of the surface, sometimes better water conditions or snow covering; indeed these localised communities seem always to be determined by some locally *favourable* conditions. Where conditions are *worse* than the average the result is an almost plantless area, a depauperation of the plateau barrens leaving only their most hardy types.

The following categories of "special localised communities" were recognised on the island:

- | | |
|------------------------|---------------------------------|
| (a) Herb communities; | (d) Marshy areas; |
| (b) Heath communities; | (e) Hillock tundra communities. |
| (c) Thick moss mat; | |

(a) *Herb communities.*

These were divided as follows:

- | | |
|------------------------------|----------------------------|
| (1) Forb ¹ areas; | (3) Wet forb-moss mat; |
| (2) Grassy areas; | (4) Dry herb-lichen areas. |

(1) *Forb areas.*

The few dry forb areas met with on the island were very small and unimportant, for while the wet forb slopes are generally bound by lush-growing mosses and hence must be described separately (see IX (a) (3) below), the dry slopes which are in sufficiently sheltered and favourable areas to have a good development of forbaceous colonists quickly become dominated by grasses, as in other parts of the world where water and temperature conditions are favourable for rapid development only in the first part of the growing season. Nevertheless occasional small flats and slopes dominated by an almost closed community of forbs were encountered, generally on sheltered patches of sand or fine detrital material near the mouths of ravines, though their transitory nature was indicated by the frequent co-dominance of several forbs, or the existence in them of families of *Epilobium latifolium*² or of one of the more aggressive grasses of such areas.

The following is a list taken from one patch:

<i>Epilobium latifolium</i> L.	a.-l.d.	<i>S. reticulata</i> L.	o.
<i>Polygonum viviparum</i> L.	a.	<i>Draba</i> spp.	o.
<i>Festuca brachyphylla</i> J. A. and J. H. Schult.	l.a.	<i>Lychnis apetala</i> L.	r.
<i>Cerastium alpinum</i> L.	f.	<i>Luzula arctica</i> Blytt	r.
<i>Poa rigens</i> Hartm. (good tufts)	f.	<i>Papaver radiculatum</i> Rotth.	(1)
<i>Salix arctica</i> Pall.	o.	<i>Pedicularis</i> sp.	(1)

(2) *Grassy areas.*

Unlike the other herb areas, which are of but local and limited occurrence, grassy communities may cover considerable tracts of the flat country towards the south-west corner of the island, where there are few watercourses and little surface drainage, and as a result of this and frequently of the situation being relatively well sheltered there are larger areas stable enough to support

¹ Clements' term for herbs other than those of grass-like habit.

² Authorities for all names will be found in "The flora of Akpatok" (10).

vegetation. There are also lakes, marshes and tracts of hillock tundra which will be described under their respective headings; the "grassy areas" are poor and scrappy, having the appearance of rough "short-grass" communities. They are most often dominated not by an actual grass but by vegetative tufts of *Carex membranopacta* L. H. Bail., with or without the large grass *Arctagrostis latifolia* (R.Br.) Griseb., which may form almost a pure society over some of the damper tracts. Still wetter areas may be locally dominated by *Eriophorum* spp., while *Salix* bushes (chiefly *S. arctica*) may be in evidence even here, though generally more important on the dry grassy areas which have a flat and stabilised surface. *Poa rigens* Hartm. and *Deschampsia alpina* (L.) Roem. and Schult. are also important grasses of these plateau areas, which have a dark humous soil even where they are no longer wet and boggy at this season.

Another type of grassy area is that resulting from the domination by true graminaceous colonists of the forb slopes described above. Such slopes have generally a dry and porous surface and in sheltered areas become covered with a loosely closed community of almost pure *Festuca brachyphylla* J. A. and J. H. Schult. or *Poa rigens*, or a mixed community dominated by these two, with or without associated forbs. The drainage is good, but little in the way of a turf can be formed before the better growing *Salices* take a hold and dominate the area. Sometimes they are torn up by the polar bears which are the only herbivores (in summer) on the island, and which seem to prefer *Salices* to grasses even in the more grassy areas, so that a kind of "pasture climax" may be maintained.

A still better grass community was the main feature of a sheltered valley which had the most luxuriant vegetation discovered on the island. This valley was near the south point and only about a quarter of a mile across, a mere shallow dip in the plateau, but instead of a frost-shattered or uneven polygon surface it had its limited plains and slight slopes composed of well-drained, fine sandy limestone material on which grasses flourished. They made a fairly close surface turf from which the larger species of *Salix* were generally excluded, while in places there was developed a distinct moss layer on the ground. The soil was mixed with a little humus penetrated by the fibrous roots of the grasses, but was still light coloured, well aerated and fairly dry. Although this was the one part of the island from which bears seemed to be absent, for even they are unable to ascend the perpendicular cliffs which extend unbroken along the coast for several miles hereabouts, some of these grassy plains looked almost like pastured meadows, and with their good moss layer and turf retentive of water, were the only example encountered on the island of a relatively dry community with two layers well developed.

The dominant grasses were *Poa alpina* L. and *P. rigens* Hartm., and in them grew *Polygonum viviparum* L.—generally abundantly, with the plants much bigger than on the plateau or even in late snow areas.

The following vascular plants were also present:

<i>Salix herbacea</i> L. (in depression with later melting snow)	l.a.	<i>Juncus castaneus</i> Sm.	o.
<i>Stellaria longipes</i> Goldie	f.	<i>Carex Bigelovii</i> Torr. ex Schwein	l.
<i>Taraxacum</i> sp. or spp.	f.	<i>Ranunculus affinis</i> R.Br.	r.
<i>Carex membranopacta</i> H. L. Bail.	o.	<i>Arabis alpina</i> L.	r.
		<i>Eriophorum polystachion</i> L.	v.r. (1)

In a little sandy depression with the surface wet from recent rain there was an open community of:

<i>Cardamine pratensis</i> L.	<i>Poa alpina</i> L.
<i>Cerastium alpinum</i> L.	<i>Ranunculus hyerboreus</i> Rottb.
<i>Equisetum variegatum</i> Schl.	<i>Pedicularis</i> sp.

(3) *Wet forb-moss mat.*

This community is developed in a few places under particularly favourable conditions near the sea. The example investigated was a slightly sloping ledge some 35 yards broad towards the bottom of the rough incline which led down to the sea at "Cove I." Except for that above the bird-cliffs (see p. 174 *et seq.*) it was the best grown example of this type of community seen and was much more luxuriant than the surrounding vegetation. It may well have been influenced by a supply of nitrates and phosphates from an Eskimo midden—a slope of barren limestone fjaeldmark strewn with skulls of bears, seals and walrus slaughtered from year to year by the Eskimo. Much carcase material must be left to rot, and it is significant that the midden lay almost directly above the ledge bearing this luxuriant community, though in between these were at least 150 ft. of rough slopes. It is most unfortunate that the source of the abundant water of this ledge was not considered, the midden and even the nitrophilous communities of the north and south of the island having been undiscovered at the time the listing was done; but the size and importance of the *Cochlearia* on it suggests a nitrophilous community, while of nine species mentioned by Summerhayes and Elton (1) as being particularly characteristic of bird-cliff areas on the north and east coasts of Spitsbergen, it is remarkable that six are frequent in this particular forb-moss mat, the other three being absent from the island or of infrequent occurrence.

There is a constant supply of fresh water to the top of the ledge, and where it percolates down a thick moss mat is developed, about 4 in. deep and continuous over the whole area, and wringing wet near the source of water. It has a gently undulating rich green surface, and consists of the closely crowded living axes of the mosses, while below lies a brown mush of decaying humous material whose pH was about 6.5. Rooted in the moss in this upper part near the water supply are a few hygrophytic vascular plants, but these are much more abundant in the lower, less waterlogged tracts where the moss nevertheless holds enough capillary water for drops to be squeezed out of any handful plucked up. Many of the angiosperms have rosettes at the level of the moss and rise little above the surface, the "field" layer as a whole being

poorly marked, though scattered grasses are always in evidence in the drier places. The following considerable list of species was made:

Chief plants, all f. to l.a.

<i>Saxifraga caespitosa</i> L.	<i>Stellaria longipes</i> Goldie
<i>S. rivularis</i> L.	<i>Cochlearia groenlandica</i> L.
<i>Equisetum arvense</i> L.	<i>C. fenestrata</i> R.Br.
<i>Saxifraga cernua</i> L.	

Other species.

<i>Polygonum viviparum</i> L.	f.	<i>Salix herbacea</i> L.
<i>Saxifraga nivalis</i> L.	f.	<i>S. reticulata</i> × <i>herbacea</i>
<i>Arabis alpina</i> L.	o.	<i>Puccinellia angustata</i> (R.Br.)
<i>Saxifraga oppositifolia</i> L.	o.	Rand. and Redf.
<i>Deschampsia alpina</i> (L.) Roem.		<i>Alsine Rossii</i> (R.Br.) Fenzl.
and Schult.		<i>Lychnis apetala</i> L.
<i>Poa alpina</i> L.		<i>Cerastium alpinum</i> L.
<i>Trisetum spicatum</i> (L.) Richt.		<i>Chrysosplenium alternifolium</i> L.
<i>Poa rigens</i> Hartm.		<i>Epilobium alpinum</i> L.
<i>Phippsia algida</i> (Soland.) R.Br.	r.	<i>Pedicularis</i> sp.
<i>Carex scirpoidea</i> Michx.		<i>Draba</i> spp.
<i>C. bipartita</i> All.		<i>Ranunculus pygmaeus</i> Wahlenb.
<i>Luzula arctica</i> Blytt	r.	<i>Veronica alpina</i> L.
<i>Juncus albescent</i> (Lange) Fernald		<i>Oxyria digyna</i> (L.) Hill
		r.
		v.r. (1)

Lichens were absent but some fungi occurred. The frequencies of the various bryophytes were not worked out, but the following seemed to be the most important, forming altogether a continuous mat:

<i>Brachythecium salebrosum</i> var. <i>arcticum</i>	<i>Camptothecium nitens</i> Schp.
Berggr.	<i>Drepanocladus uncinatus</i> (Hedw.) Warnst.
<i>Bryum</i> sp.	<i>Mnium affine</i> var. <i>rugicum</i> B. and S.

The following were of more casual occurrence:

<i>Marchantia polymorpha</i> L.	<i>Mnium affine</i> Bland.
---------------------------------	----------------------------

Of fungi there were several Agaricaceae and one Polyporaceous species.

(4) *Dry herb-lichen areas.*

While no proper "reindeer moss" communities occur on the island—both its main constituents *Cladonia rangiferina* and *C. sylvatica* appear to be absent—occasional sheltered tracts of the more stable south-west plateau have patches dominated by a close mat of upright-growing *Cladoniae*, *Cetrariae* and other ground lichens. The following example, listed from near the bird-cliffs in the south, was not quite typical; it was a more extensive community of herbs in which *Dryas* (really woody) was the main plant, in slight tussocks covering about a quarter of the area. But the ground between, even around the bases of the other angiosperms, was covered with a continuous investment of light-coloured lichens, so that the area had the appearance of true lichen tundra. We may note the occurrence of the well-known ground lichens *Cladonia uncialis* Web. and *Alectoria ochroleuca* Nyl. (2), though *Ochrolechia tartarea* and *Cetraria nivalis* were the most abundant species. Lichens formed only a thin surface crust, the subsoil being rich though dry, dark brown, humous and distinctly acid (pH 6.0–6.5).

The community was listed as follows; no bare stones occurred suitable for colonisation by the usual crustaceous lichens:

ANGIOSPERMS

<i>Dryas integrifolia</i> Vahl	a.-d.	<i>Luzula arctica</i> Blytt	f.
<i>Poa rigens</i> Hartm. (in depressions)	l.a.	<i>Salix reticulata</i> L.	l.
<i>Arotagrostis latifolia</i> (in depressions)	l.a.	<i>Carex misandra</i> R.Br.	o.
<i>Polygonum viviparum</i> L.	f.-l.a.	<i>Saxifraga oppositifolia</i> L.	o.
<i>Salix arctica</i> Pall.	f.	<i>Cerastium alpinum</i> L.	o.
<i>Pedicularis</i> sp.	f.	<i>Saxifraga nivalis</i> L.	r.

LICHENS

<i>Ochrolechia tartarea</i> Massal.	v.a.	<i>A. divergens</i> Nyl.
<i>Cetraria nivalis</i> Ach.	v.a.	<i>Physcia muscigena</i> Nyl.
<i>Alectoria ochroleuca</i> Nyl.	a.	<i>Cladonia uncialis</i> Web.

Mosses as a whole are little in evidence, though the following may be abundant in slight depressions:

<i>Hylocomium rugosum</i> De Not.	<i>Tortula ruralis</i> Ehrh.
<i>Swartzia inclinata</i> Ehrh.	

There are suggestions in the above lists that the community was somewhat influenced by the proximity of the bird-cliffs.

(b) *Heath communities.*

Besides the undoubted late snow areas of *Cassiope* described under VII (b)¹, there exist on the island occasional more extensive heathy tracts dominated by this and other Ericaceae, and in the most favourable localities by *Empetrum*. A good snow covering appears to be essential, the soil being dark and humous beneath the close mat formed by the woody plants and their associated mosses and lichens. Sometimes in less favourable localities willows replace the usual heathy dwarf-shrubs, the outstanding example being the *Salix*-moss mat described below, but still the area has the appearance of a heath, and like the other types distinguished thins out to one of the usual open plateau communities at its less sheltered edges.

The following "heathy" mats were distinguished, and though transitional stages and mixed ground-shrub mats occur, resemble most other closed communities in covering but a small portion of the area of the island:

- (1) *Empetrum* mat,
- (2) Dry *Cassiope*-lichen mat,
- (3) *Salix*-moss mat.

(1) *Empetrum* mat.

On the whole *Empetrum* is unimportant on the island, for though it occurs in many of the more sheltered regions near the shore, and occasionally on the plateau, it rarely dominates more than small patches of the better type of *Cassiope* heath. Nevertheless some examples of a true and almost pure *Empetrum* mat do occur, most notably on gentle sheltered slopes of the relatively stable and well-vegetated south-west portion of the island, and around the shores of Cove I on the south-east coast (9). The example listed was developed in the shelter of a rocky ridge at an altitude of about 600 ft. Its

¹ See "The vegetation of Akpatok Island, Part I" (4).

area was small, being limited by that of winter snow covering, but the community is worthy of special note because of the importance of the dominant in other northern regions, and its possible significance as an indicator plant.

Empetrum flourishes best on an acid soil; it is only in bogs and certain sheltered places where vegetation is especially good that such acidity can develop on the everlasting limestone of Akpatok. The soil below the litter of the *Empetrum* mat listed was thick and humous, dark and damp, and with an acidity extending to pH 6.0.

The *Empetrum* was in full berry—black, ripe and in places abundant—though it must be remembered that this was an exceptional year, the Eskimo at Port Burwell reporting that they had never before seen so many berries. In Lapland at this season (end of August) the year before, the berries were more or less over, the seasons being very much earlier there, and in Spitsbergen, though the plant is rare and does not normally ripen fruit ((1), p. 263), ripe berries have been seen by Clutterbuck on August 16th. Actually the seasons on Akpatok are earlier than in Spitsbergen but much later than on the Labrador coast not far to the south.

The *Empetrum* shoots on Akpatok are never more than 3 in. high and generally less than 2 in., but though the plant seems to be eking out a precarious existence under the peculiar climatic and (partly resulting) edaphic conditions, it is in places sufficiently aggressive to form this close mat, intermixed with *Salix* spp., *Dryas* and a few herbs. The majority of the associated plants in the list given below flower best towards the outer limits of the *Empetrum* mat, which in places towards the centre ousts them almost entirely.

ANGIOSPERMS

<i>Empetrum</i> sp. (in berry)	v.a., d.	<i>Carex membranopacta</i> L. H. Bail.	o.
<i>Dryas integrifolia</i> Vahl (small tufts, suppressed)	a.	<i>Polygonum viviparum</i> L.	o.
<i>Salix reticulata</i> L.	f.	<i>Salix arctica</i> Pall.	r.
<i>Vaccinium uliginosum</i> var. <i>microphyllum</i> (in berry)	f.	<i>Bartsia alpina</i> L.	l.
<i>Cassiope tetragona</i>	f.	<i>Carex scirpoidea</i> Michx.	r.
<i>Saxifraga oppositifolia</i> L.	o.	<i>Pedicularis</i> sp.	r.
		<i>Oxyria digyna</i> (L.) Hill	(1)

. Though several of the species of the rather poorer *Cassiope* heath occur, mosses and lichens are little in evidence except where the *Empetrum* is less thick and overwhelmingly dominant: here *Cassiope*, *Dryas* and *Salices* become more important and the community is of a mixed heath type. One example from which *Empetrum* was absent had both lichens and mosses very abundant, forming a mat transitional to the dry *Cassiope*-lichen mat described below. Its main angiosperms were the following:

<i>Cassiope tetragona</i>	d.	<i>S. herbacea</i> L.
<i>Dryas integrifolia</i>	a.	<i>Carex misandra</i>
<i>Salix reticulata</i> L.	f.	<i>C. membranopacta</i>
<i>Vaccinium uliginosum</i> var. <i>microphyllum</i>	f.	<i>C. scirpoidea</i>
<i>Rhododendron lapponicum</i> (L.) Wahl.		<i>Luzula arctica</i> Blytt
<i>Salix arctica</i>		<i>Tofieldia borealis</i>
		<i>Poa</i> sp.

There is little doubt that the first heath described, that in which *Empetrum* is overwhelmingly dominant or almost pure, is the climax community of more favourable localities—a post-climax if the whole area of the island is being considered. The open *Dryas-Salix*, etc., community of the plateau is the real Akpatok climax—maintained as an edaphic sub-climax if we consider it as part of the Hudson Strait patchwork, and, in places where these are most unfavourable, reduced even further by topographic (exposure) and geodynamic (polygon, scree, etc.) conditions. Though dominated by it at high altitudes in Lapland (3), *Empetrum* suppresses *Cassiope* wherever it can get a hold on Akpatok. This may be due in part to the notorious inability of *Cassiope* to stand fogs, though the mere fact that it is dominant in places on Akpatok suggests that it may be less sensitive to fogs than has been supposed.

(2) *Dry Cassiope-lichen mat.*

In spite of the fogginess of the island this occurs over areas less limited than the *Empetrum* mat though perhaps less frequently than the mixed heath type. It varies in appearance (though little in phanerogam composition) according to whether the ground is damp enough in the early part of the growing season for tussock-forming mosses: in such cases the *Cassiope* grows taller and lichens are largely replaced, though the ground is generally quite dry by the end of August. A still drier, smooth *Cassiope*-lichen mat is frequently met with on slopes which are so sheltered by a ridge that snow more or less covers them in winter—but is apparently not deep enough for its water to last late into the summer. Some patches, where *Cetraria nivalis* is abundant, are probably bare of snow in winter.

The *Cassiope* axes are short, never rising more than 3 in. above the soil surface, while they are much interspersed with other ground-shrubs, especially *Vaccinium uliginosum* var. *microphyllum*. Growing level with the *Cassiope* to form a smooth quilt is a continuous investment of the lichens listed, *Stereocaulon alpinum* blending with the abundant dead axes of the *Cassiope* to give the ground a greyish appearance, in places relieved by plentiful white thalli of *Cetraria nivalis*. Below, and binding all together, are mosses, though they rarely show at the surface in this drier type; in the example listed they made the ground springy to the step, the vegetation often being as much as 3 in. deep, with only the tips of the *Cassiope* axes showing at the surface. It seems likely that the particular example listed was a case of regression—from a better type of *Cassiope* mat with mosses to a poorer one with lichens—resulting from a change from a good snow covering (cf. the *Cassiope* zone of a late snow patch (4)) to a poorer one as some factor of the environment changed in time. The mosses persisted below, but their tussocky tops were colonised by lichens (e.g. *Cetraria nivalis*) which now form a stable crust in which the *Cassiope* may in places be but little in evidence: indeed the majority of its shoots are dead or dying, a fact which supports the regression hypothesis.

ANGIOSPERMS

<i>Cassiope tetragona</i> (L.) D. Don.	d.	<i>Chrysanthemum integrifolium</i> Rich.	r.
<i>Vaccinium uliginosum</i> var. <i>microphyllum</i>	a.	<i>Tofieldia borealis</i> (Wahl.) Wahl.	r.
<i>Dryas integrifolia</i> Vahl	a.	<i>Pyrola rotundifolia</i> var. <i>pumila</i>	r.
<i>Salix reticulata</i> L.	f.	Hook.	
<i>Empetrum</i> sp.	o.	<i>Carex misandra</i> R.Br.	r.
<i>Polygonum viviparum</i> L.	o.	<i>C. scirpoidea</i> Michx.	r.
		<i>Juncus albesens</i> (Lange) Fernald	r.

LICHENS

<i>Cetraria nivalis</i> Ach.	l.a.	<i>Peltigera malacea</i> Fr.	o.
<i>Stereocaulon alpinum</i> Laur.	a.	<i>Ochrolechia tartarea</i> Massal.	o.
<i>Cetraria hiascens</i> Th. Fr.	a.	<i>O. tartarea</i> var. <i>frigida</i> Kbr.	
<i>C. islandica</i> var. <i>tenuifolia</i> (crispa) Wain.	f.	<i>Thamnolia</i> (Cerania) <i>vermicularis</i> S. F. Gray	
<i>Cladonia mitis</i> Sandst.	f.	<i>Pertusaria dactylina</i> Nyl.	

Bryophytes: the following were all fairly abundant; also a protonemal growth which appeared to belong to another type:

<i>Dicranum Muhlenbeckii</i> B. and S.	<i>Myurella julacea</i> B. and S.
<i>Hedwigia ciliata</i> Ehrh.	

This community thins out to a stony *Dryas* slope on which a little *Cassiope* persists, with some *Silene acaulis* L. and *Carex scirpoidea* and many grey lichens, though otherwise it is like the poorer, dry valley type V (b) (see (4), p. 379).

(3) *Salix-moss mat.*

This is a totally different type, fairly dry but heathy only in appearance. It is developed on areas which must have a good snow covering and which probably remain wet until late in the growing season. The example listed was vegetation of a luxuriance rarely encountered on the island except where the nitrogen deficiency was made good by nesting birds; though covering a considerable area on a sheltered slope it appeared to be a peculiar zone of a large snowdrift area, for it merged above into a *Dryas-Cassiope* region with mosses, and below was bounded by a distinct tract of *Salix herbacea*.

The mosses binding the mat show little tendency to form tussocks, the surface being flat but springy to walk upon, for the moss growth is often as much as 8 in. deep. The dominants are *Aulacomnium papillosum* Jaeg. and *Philonotis fontana* Brid., and together they form an almost continuous mat, except where occasional boulders project, covered with a close investment of *Cladonia pyxidata* var. *pocillum*.

The willows root in the mosses or their dead bases, where the humous matter is damp and very slightly acid, while the stems with their adventitious roots run as rhizomes beneath the surface of the moss, so that only the leaves appear on the surface. The main dominants are *Salix arctica* and *S. reticulata*, both abundant and much mixed; herbs on the other hand are little in evidence, and though the following occur only *Polygonum viviparum* is at all abundant:

<i>Polygonum viviparum</i> L.	a.	<i>Equisetum variegatum</i> Schl.	
<i>Poa rigens</i> Hartm.		<i>E. arvense</i> L.	
<i>Stellaria longipes</i> Goldie		<i>Dryas integrifolia</i> Vahl	v.r. (1)

(c) Thick moss mat.

Besides the moss mat covering considerable tracts above the bird-cliffs at the north and south ends of the island, a thick moss mat is developed in certain situations where abundant percolating water lasts well into the growing season, for example towards the centre of a long-lasting snowdrift. The mat may be anything from 1 to 8 in. thick according to water and other conditions, while the length of the growing season of the particular area is also important, being greatly reduced where the snow melts late, so that the mosses are anaemic and of poor growth. Most often the mat is 2-4 in. thick, and being supplied with water from limestone crags or melting snow is alkaline or neutral, though generally dark and humous within.

The types will not be described in full since the main examples or their nearly related facies are considered elsewhere, while the reasons for the dominance of one or another of the various mosses which were important in these thick mats were not properly worked out. Again the mats are of very limited occurrence except in the case of the damp bird-cliff type, and are better considered as special localised communities; examples are described under VII (b) (see (4), p. 389), IX (a) (3), p. 164 and IX (b) (3), p. 169) (these are all colonised by angiosperms except in the very wettest places where a pure moss mat may occur); also X (b) (p. 175 *et seq.*) and some of the temporary freshwater communities described under XI (a) and (b) (pp. 179-183 below).

(d) Marshy areas.

These vary according to the extent and permanence of their water supply and also according to exposure. The better vegetated bogs developed in sheltered valleys such as that discovered near the south end of the island have already been described under VI (a)¹, so we may here limit ourselves to an account of the shallower marshes which occur in dips and near lakes on the plateau, and occasionally on level shelves on the sides of the less-sheltered valleys. The vegetation is generally much more luxuriant than on surrounding areas, for its poorer beginnings in small damp depressions of the plateau (described under II (c)¹) were already a great advance on the rest of the plateau. Pl. XXXIX, phot. 37, in Part I (4) shows one type of marshy area, though this in places is almost dry by the end of August and is of the hillock tundra type (see IX (e) below).

Pl. XVII, phot. 1, shows a mixture of barren plateau, marshy waterside, damp hillock tundra and, on the right-hand side at the level of the figure, a tract of deeper cotton-grass (*Eriophorum*) bog. Unlike most parts of the island, where the vegetation is poor and dependent upon local conditions of physiography, exposure and snow covering, the marshes and bogs (and to a lesser extent the hillock tundra areas) have a closed vegetation and are peculiar in being generally dominated by one species to the exclusion of others. In ordinary

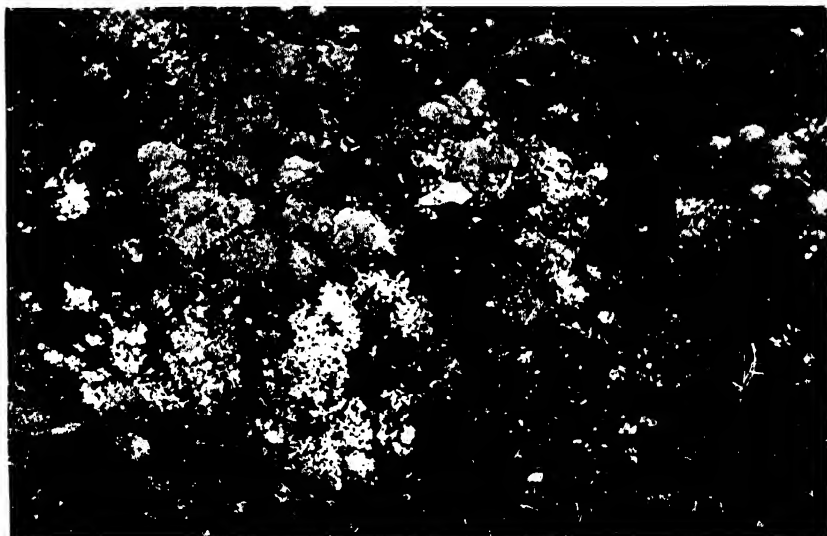
¹ See "The vegetation of Akpatok Island, Part I" (4).



Phot. 1. Drastic changes of vegetation on plateau: barrens, marshy waterside, damp hillock tundra (in foreground) and cotton-grass bog (on right) all near together (p. 170).



Phot. 2. Bed of stream (largely barren) with erratic boulder of mica schist more worn and less vegetated on left-hand side facing upstream. The water is low in late summer (p. 183).



shallow marshy dips which may be almost dry by the end of summer, *Carex membranopacta* is the chief plant and often the only one. In wetter places *Deschampsia alpina* and *Arctagrostis latifolia* may be abundant. Long upright axes (30 cm.) of the latter are seen in front of the open water in the photo, and often form pure communities in habitats with a deeper, more stable humous soil. In the deepest and wettest bogs cotton-grasses are usually dominant, either *Eriophorum Scheuchzeri* or *E. polystachion* forming a more or less pure community, though sometimes they may be mixed and include grasses, sedges, and in drier places occasional willows.

Alopecurus alpinus Sm. occurred only round one lake on the island, so far as it was explored by the writer, but (except for a little *Pleuropogon Sabinei* R.Br.) it dominated exclusively the peculiar marshy habitat produced where fresh water sometimes percolated from the lake into a smaller pool.

These marshy areas rarely have any of their smooth humous surface left undominated by one or other of the above-mentioned species, and there are few other typical marsh or fen plants on the island. Mention should, however, be made of the very wet earthy tracts occupying some depressions in the plateau. They may have their vegetation locally closed by one of the above-mentioned types, but generally they bear an open community with abundant *Carex membranopacta*, *Arctagrostis latifolia*, etc.; while growing in the damp earthy gaps between these larger plants are a number of smaller ones chiefly characteristic of deep and waterlogged soils, though these are here light coloured and not acid. The area may be not unlike that described under III (d) ((4), p. 372) but is flat and stagnant, with a more stable and much better vegetation and corresponding greater admixture of humus in the soil. The following are the more typical plants of such situations:

<i>Arctagrostis latifolia</i> (R.Br.) Griseb.	<i>Oxyria digyna</i> (L.) Hill
<i>Braya purpurascens</i> (R.Br.) Bunge	<i>Phippsia algida</i> (Soland.) R.Br.
<i>Carex bipartita</i> All.	<i>Poa alpina</i> L.
<i>C. membranopacta</i> L. H. Bail.	<i>Ranunculus pygmaeus</i> Wahlenb.
<i>Epilobium alpinum</i> L.	<i>Saxifraga caespitosa</i> L.
<i>Equisetum arvense</i> L.	<i>S. cernua</i> L.
<i>E. variegatum</i> Schl.	<i>S. stellaris</i> L. var. <i>comosa</i> Retz.
<i>Eriophorum polystachion</i> L.	<i>S. tenuis</i> (Wahlenb.) H. Sm.
<i>Juncus albesens</i> (Lange) Fernald	<i>Tofieldia borealis</i> (Wahl.) Wahl.
<i>J. biglumis</i> L.	<i>Kobresia simpliciuscula</i> (Wahl.) Mackenz.

(e) *Hillock tundra communities.*

Much of the damp, vegetated foreground in Pl. XVII, phot. 1, is made up of hillock tundra (5), whose main feature is the irregularity of the surface, thrown up at intervals into little rounded hummocks which on Akpatok never seem to exceed 1 ft. in height or 2 ft. in breadth. They appear in areas which are fairly damp, at least in early summer, and have some depth of fine soil; Sukachev (6) ascribes their formation to frost action. The lower layers of soil contain ground ice (here they are generally of flat limestone rock), and when the upper layers freeze in autumn the soil becomes compressed between the

two hard layers of ice, till it is arched up by increasing internal pressure due to expansion of water on freezing, and masses of earth are forced out through ruptures in the surface layer. In summer these heaps of damp earth are rapidly colonised by plants and give rise to mossy or other hillocks. The little dips between may be much less vegetated, remaining wet and boggy from late-melting snow and supporting only an open community of bog plants.

On Akpatok the hillocks are all small, and even those in dips on the exposed plateau are apparently wholly covered with snow in winter. They exhibit as a rule neither zones of vegetation indicating a microclimatic difference between their tops, sides and the intervening dips, nor the feature of drying out of the top and regression to a lichen stage owing to the difficulty experienced by the plants in raising water to the top as the hillock grows higher both by the pushing up of soil from below and by the addition of humous material from above. The hillocks are small and their area is almost uniformly vegetated by either *Carex membranopacta* L. H. Bail., *Eriophora* or one of the usual grasses of such damp situations (see IX (d), pp. 170-171).

On the other hand there occur, in some more sheltered valley regions, limited hillock tundra areas where the hillocks are broader and damper, and the vegetation more luxuriant though mixed. One example investigated was developed on a slightly sloping ledge partway down the side of a valley. It was supplied with a continuous flow of fresh water in summer by a brook entering its upper end, and thus the tracts between the hillocks were damp. The tops of the hillocks were dry and slightly acid, showing stages of succession to *Dryas* and even mixed *Cassiope* heath, while *Salices* were fairly abundant and in some cases rooted in the damper dips, growing up the 8 or 10 in. to the level of the tops of the little hillocks, which may perhaps in this case have been blown bare of snow in winter.

Lichens and mosses were again little in evidence, though the latter in places formed good tufts. The vascular plants were listed as follows, most of the shrubby types occurring only on the drier tussocks with flat tops:

<i>Carex membranopacta</i> L. H. Bail.	d.	<i>Polygonum viviparum</i> L.	f.
<i>Dryas integrifolia</i> Vahl	a.	<i>Salix reticulata</i> L.	f.
<i>Cassiope tetragona</i> (L.) D. Don	l.a.	<i>Tofieldia borealis</i> (Wahl.) Wahl.	o.
<i>Equisetum variegatum</i> Schl.	l.a.	<i>Saxifraga aizoides</i> L.	o.
<i>Salix arctica</i> Pall.	f.	<i>Rhododendron lapponicum</i> (L.) Wahl.	r.
<i>Vaccinium uliginosum</i> var. <i>microphyllum</i> f.			

Musci

Catascopium nigrum Brid.
Camptothecium nitens Schp.

Swartzia montana Lindb.

X. SPECIAL LOCALISED HABITATS.

(a) *Morainic accumulations of siliceous soils.*

Besides the erratic boulders already described, there are on the plateau occasional conically shaped "drumlins" of quartz sand left by glaciers receding after the last glacial phase, and one or two more extensive moraines of mixed sand and boulders. The conical drumlins are most abundant towards the

south-west end of the island, being absent from the north. They are quite small, rising generally no more than 8 or 10 ft. above the level of the surrounding plateau, but are very distinctive, their sides being steep and scree-like though smooth and well vegetated, while their tops are almost always surmounted by a conspicuous tuft of grass. This owes its good growth to the ptarmigan which are frequent on the barrens in summer: they need quartz sand for their gizzards and repair to such deposits, generally squatting on the top so that their droppings fall around. *Festuca brachyphylla* J. A. and J. H. Schult. and *F. rubra* var. *arenaria* (Osb.) Fr. are the chief grasses, and may clothe even the sides of the mound with a continuous investment. In this *Polygonum viviparum* may be fairly abundant, though the sand is very coarse and the habitat too dry and exposed for the usual nitrophilous plants such as *Cochlearia*.

The occasional more extensive morainic deposits of boulders, sandy quartz particles, and some finer soil are better vegetated than any other part of the plateau, supporting a thick and almost continuous community including nitrophilous types, except where there are bare and dynamic tracts of white sand¹. The "Black Ridge"² is the biggest morainic deposit on Akpatok, rising about 60 ft. above the highest plateau in the middle of the island. Unfortunate circumstances prevented the present author from returning to the region to work more carefully on its peculiar communities, but the following notes made on a short exploratory visit may be taken as a guide to the general type, while the appended list of the plants collected there is significant.

From a distance the ridge looks dark in colour contrasted with the surrounding limestone plateau. This is partly due to the black boulders of mica schist giving it a rugged outline where the boulders have been left clear by washing away of the sand among which they were deposited, and partly to the much better vegetation the whole area supports. Apart from interruption by these boulders and the occasional patches of coarse white sand¹, the vegetation is continuous in spite of the extremely exposed situation; though it is true that a snow covering for the areas between is probably held by the boulders. Several of the angiosperms and lower plants occurring here were found nowhere else on the island, while others seem to be confined elsewhere either to the smaller morainic accumulations with a tendency to acidity or else to the peculiar bird-cliff areas described in the next section.

In the shelter of the larger erratic boulders on the ridge, a fair approximation to a "reindeer moss" community dominated by *Cladonia* spp. may be developed. The axes are upright and closely packed, and though the community includes several mosses and a liverwort, these are altogether subsidiary to the lichens:

BRYOPHYTES

Pogonatum septentrionale Röhl.
Rhacomitrium lanuginosum Brid.

Timmia bavarica Hessel.
Ptilidium ciliare (L.) Hpe.

¹ Probably secondary "blow-outs."

² See plate facing p. 218 in *The Isle of Auks* (9).

LICHENS

Cladonia amaurocrea Schaer.

C. mitis Sandst.

C. pyxidata Hoffm. var. pocillum Wain.

Cetraria hiascens Th. Fr.

C. islandica Ach. var. tenuifolia (crispa)

C. nivalis Ach.

Ochrolechia tartarea Massal. var. frigida Kbr.

In other places *Pogonatum septentrionale* and *Rhacomitrium lanuginosum* form a thick mossy carpet, while *Salix herbacea* L. and *Harrimanella* (*Cassiope*) *hypnoides* (L.) Coville are locally abundant, the latter sometimes forming a continuous mat. Species of *Luzula* and of *Potentilla* and *Erigeron uniflorus* L. are more frequent than anywhere else on the island; the *Pyrola*, again, is here more aggressive than anywhere else, with abundant runners and even occasional flowers.

Under all these denser patches of vegetation the soil, though light-coloured and gritty, is damp and distinctly acid, generally about pH 5.5.

The following are the more peculiar plants collected. Many are markedly calcifuge while on the other hand several of the chief plants of the surrounding plateau seem to be absent, including *Dryas*, *Saxifraga oppositifolia*, *S. aizoides* and even *Salix arctica*. In fact, except for such ubiquitous types as *Polygonum viviparum*, the vegetation is almost entirely composed of the following list of plants which are absent from the general plateau. The list gives some indication of the comparative richness of the flora on acidic rocks even in such an exposed situation, though this richness may in part be due to the relieving of an otherwise acute nitrogen problem by ptarmigan which visit the deposit for grit.

Alsine Rossii (R.Br.) Fenzl

Antennaria sp.

Arabis alpina L.

Arctostaphylos alpina (L.) Spreng.

Braya purpurascens (R.Br.) Bunge

Carex bipartita All.

Cassiope tetragona (L.) D. Don.

Cerastium alpinum L.

C. trigynum L.

Chrysanthemum integrifolium Rich.

Cochlearia fenestrata R.Br.

C. groenlandica L.

Diapensia lapponica L.

Forms of Draba including

D. alpina L.

D. lactea Adams vel fladnizensis × lactea

Empetrum sp.

Epilobium alpinum L.

Erigeron uniflorus L.

Eutrema Edwardsii R.Br.

Festuca brachyphylla J. A. and J. H. Schult.

Harrimanella hypnoides (L.) Coville

Luzula arctica Blytt

L. hyperborea R.Br.

Lychnis apetala L.

Lycopodium Selago L.

Papaver radiculatum Rotth.

Pedicularis sp.

Phippsia algida (Soland.) R.Br.

Poa alpina L.

Potentilla alpestris Hall, forma

P. emarginata Pursh.

P. tridentata Soland.

Puccinellia angustata (R.Br.) Rand and Redf.

Pyrola rotundifolia var. pumila Hook.

Ranunculus pygmaeus Wahlenb.

Salix herbacea L.

S. reticulata L.

Saxifraga caespitosa L.

S. stellaris L. var. comosa Retz.

S. tenuis (Wahlenb.) H. Sm.

Vaccinium Vitis-Idaea L.

Veronica alpina L.

(b) Bird-cliffs.

Countless pairs of guillemots visit the island in summer to nest: in fact the island is named after them in that *Akpat* is Eskimo for a guillemot or "auk" and *ok* means an island. Their nesting sites seem to be confined to the exceptionally high perpendicular cliffs which run for some miles round the south and north-east ends of the island (see map on p. 339 of Part I (4)), and there



Phot. 5. Harp Cove lagoon at low spring tide: shingle bar and sea on right (p. 184).



Phot. 7. Akpatok cliff seen from broken part of limestone shelf uncovered at low tide. Cliff base smoothed and undermined by wave action (p. 187).



Phot. 4. Bird-cliffs with tops stabilised by luxuriant vegetation, so that they are not rounded but remain flat to the edge (p. 175). Photograph taken from cliff-top, with sea 600 ft. below.



Phot. 6. Typical Akpatok coast at low spring-tide: note small light-coloured shingle bank in angle between cliff base and outgoing horizontal limestone shelf (pp. 185 and 187).

they occupy every ledge and cranny to within a foot or two of the cliff-top. From the congested ledges light-coloured strips of excrement and fish debris extend down the cliffside, apparently for the most part hardened into a guano-like substance, though always smelling abominably, emitting in fact a stench which is intolerable even on the plateau above.

Unlike the other cliffs, which are bare, these bird-cliffs have every ledge and cranny supporting some form of vegetation, except of course where there is actual trampling by birds, and lush green tufts of grass or *Cochlearia* wherever there is a heap of droppings or an impingement of nitrate-bearing water coming from one of the filthy ledges. It is unfortunate that their inaccessibility prevented closer investigation of these cliff faces; nor were the screes which in one or two places existed below them visited, though they were noticeable from the sea because of the rich dark strips of vegetation which they support in places where they are manured by the incoming and outgoing birds.

The cliff-tops above the nesting birds are unlike those of any other part of the island. Instead of being rounded and almost barren they are well vegetated with one of a peculiar series of tundra communities, which stabilise them so that they are flat to the edge in spite of the extremely exposed situation (see Pl. XVIII, phot. 4). In type and lushness this vegetation is a very remarkable phenomenon; that it is dependent on the proximity of the nesting birds is evident from the fact that it stops opposite any point at which there are no nests; but though in type it appeared nitrophilous, the exact way in which it is dependent on the birds was much more obscure, for guillemots never visit the tops of their nesting cliffs. Generally there was a thick mat of mixed mosses and lichens (Pl. XVII, phot. 3), or, in any damper depressions, of mosses without lichens; and in this mat there were rooted numerous small angiosperms including *Cochleariae* of good growth and much *Poa rigens* Hartm. It seemed possible that lichens, susceptible as they are to fumes in the atmosphere, might collect nitrogenous material from the foul vapours (and doubtless sometimes dust) rising from the bird-cliffs, especially as the rough limestone boulders sometimes strewn about the edge were almost covered with crustaceous lichens or more often with the well-known foliose *Xanthoria* (*Lychnea*) *candelaria* Arn. together with *Caloplaca elegans* Th. Fr. and *Anaptychia ciliaris* Massal. Such lichens might be the first colonists, bringing to the soil just that modicum of combined nitrogen necessary to allow other plants to go ahead. Another suggestion was that drops of water with nitrates and phosphates in solution in wet weather, or even solid guano in dry, might be blown off the face of the cliffs and deposited on their flat tops, for the gales were of such force that in one place the water from a stream gushing over the cliff-top was observed to be blown back and deposited as spray some yards behind the edge of the cliff [(9), p. 176].

Actually the vegetation seemed more luxuriant than the first suggestion could easily allow, and since it often stretched nearly 100 yards from the

edge of the cliff, was surely too extensive to be explained by the second alone. It appeared that some more potent force must be at work, and the clue was given on discovering in places pieces of eggshell lying about, while the "patchwork quilt" was here dotted with feathers clinging to grass axes or half buried in the moss tussocks. Glaucous gulls are fairly numerous around these bird-cliffs and are known to live on the eggs and young of nesting guillemots, which they carry up to the cliff-tops to consume. Snowy owls and Peregrine falcons are also there, and the latter probably carry off the old birds; in fact in the north of the island occasional bones and dried up pieces of skin were found, besides numerous eggshells and feathers, and excreta and other signs of foxes and bears. Here then are the sources of nitrogenous and phosphatogenous food materials, and a further source must be the droppings of the birds of prey which congregate above the bird-cliffs, and also of occasional scavenging ravens.

With what is thus almost certainly an abundance of available nitrogen, at least in comparison with other parts of the plateau where it is so deficient as probably to limit growth, the vegetation along the tops of the bird-cliffs is extremely luxuriant. The flora is very uniform, the usual type markedly so at the two ends of the island. Though there can be little or no snow covering in winter, this usual type is a luxuriant "patchwork quilt" of mixed mosses and lichens. The "quilt" forms a thick covering to the ground, above which it rises as a dense growth for 4 to 6 in., and it is a many-coloured patchwork because the lichens which grow in fine patches on or among its green or red-brown mosses are of such varying colours as light green, brown, white and yellow. The surface is slightly undulating rather than tussocky. Beneath the close investment of living mosses very retentive of water is a brown, mushy (at least in wet weather) humus layer whose *pH* is very slightly acid. This composes the lowest 2-3 in. of the mat, while rooting for the most part in the surface are numerous though scattered small rosette and other angiosperms. The following is a list from a small area above the southern bird-cliffs:

Musci form an almost complete investment, chiefly

Dicranum groenlandicum Brid.
D. Muhlenbeckii B. and S.

Tortula ruralis Ehrh.

Lichens form patches on or among the mosses, the patches often being as much as 6 in. in diameter though generally composed of a single species having its own individual (and often quite striking) colour, although this may vary with the weather, according to whether the squamules are wet or dry:

Alectoria divergens Nyl.
A. ochroleuca Nyl.
Cetraria islandica var. *tenuifolia* (crispa)
C. nivalis Ach.

Cladonia mitis Sandst.
Ochrolechia tartarea Massal. var. *frigida* Kbr.
Sphaerophorus globosus A. L. Smith
Thamnolia (*Cerania*) *vermicularis* S. F. Gray

Angiosperms:

Cochlearia groenlandica L.
C. fenestrata R.Br.
Poa rigens Hartm.
Saxifraga tricuspidata Rottb.
Cerastium alpinum L.
Polygonum viviparum L.

a.
a.
a.
l.a.
f.
f.

Saxifraga oppositifolia L.
Draba spp.
Salix arctica Pall.
Stellaria longipes Goldie
Lychnis apetala L.

o.
o.
r.
r.
v.r.

On the northern bird-cliffs the angiosperms are generally those of the above list except for the apparent absence of *Saxifraga tricuspidata*, whose place is taken by *S. caespitosa*, while *Poa rigens* is especially abundant. In addition there may occur in places:

Alsine Rossii (R.Br.) Fenzl
Arctagrostis latifolia (R.Br.) Griseb.
Cerastium trigynum Vill.
Chrysosplenium alternifolium L.
Draba oblongata forma

D. Bellii (forma ad *D. oblongata*)
Festuca rubra var. *arenaria* (Osb.) Fr.
Saxifraga caespitosa L.
S. Hirculus L.

The lichens of the cliff-top communities of the north are also almost identical with those of the south, though we might add to the above typical list *Cetraria cucullata* Ach., *C. hiascens* Th. Fr. and *Physcia muscigena* Nyl. The mosses on the other hand are generally different in species though not in growth, for *Tortula ruralis* Ehrh. and *Aulacomnium turgidum* Schwaeagr. seem to be the only important mosses common to the north and south cliff-tops, the chief additional species in the north being:

Ditrichum flexicaule Hampe
Thuidium abietinum B. and S.

Brachythecium salebrosum var. *arcticum*
 Berggr.

Any damper area, such as a slight depression in this patchwork mat, has the mosses more overwhelmingly dominant, and in the most favourable localities almost pure. In one example in the north the feet sank as much as 8 in. into the mat, which below its soft luxuriant living surface was of wet mushy light-brown humous material, very slightly acid (pH 6.5). *Brachythecium salebrosum* var. *arcticum* and *Tortula ruralis* between them covered the area, each forming slight tussocks. Lichens were absent and vascular plants relatively unimportant, though the following occurred:

Cerastium trigynum Vill.
Draba sp.
Lycopodium Selago L.
Poa rigens Hartm.

Polygonum viviparum L.
Saxifraga caespitosa L.
S. Hirculus L.

In Pl. XXX, phot. 9, in Part I (4) we see an immediate difference between the "giant polygons" which support a patchwork quilt, and their separating dips which are clothed with mosses alone. On the edge of this peculiar polygon area conditions are drier and lichens more abundant, while the dips are shallower and have grasses and some lichens growing among the mosses.

Where the nests are fewer or extend less far up the cliff face, so that the region is less visited by birds of prey and scavengers, there is developed instead of the lush patchwork quilt a dry open fjaeldmark community of angiosperms with much *Dryas*; and the cliff-edge, not being completely stabilised by vegetation, is rounded and crumbly. Influenced to some extent by the birds, the flora is large, but the community is open and rather poor, consisting of the following angiosperms, with hardly any mosses or lichens.

<i>Dryas integrifolia</i> Vahl	a.	<i>Poa rigens</i> Hartm.
<i>Alsine Rossii</i> (R.Br.) Fenzl		<i>Polygonum viviparum</i> L.
<i>Arabis alpina</i> L.		<i>Potentilla alpestris</i> Hall forma
<i>Astragalus alpinus</i> L.		<i>P. nivea</i> L.
<i>Cerastium trigynum</i> Vill.		<i>Salix arctica</i> Pall.
<i>Epilobium latifolium</i> L.		<i>Saxifraga oppositifolia</i> L.
<i>Festuca rubra</i> var. <i>arenaria</i> (Osb.) Fr.		<i>S. tricuspidata</i> Rottb.
<i>Lychnis apetala</i> L.		<i>Silene acaulis</i> L.
<i>Oxytropis podocarpus</i> A. Gray		

Intermediate between this fjaeldmark community and the patchwork quilt, and often dominating the cliff-top, is the more familiar *Dryas* mat with associated willows, etc. This community also in many places forms a transition between the patchwork quilt and the ordinary poor vegetation of the unaffected plateau behind; while patchwork may pass abruptly into ordinary plateau it is more frequent to find zonation, in which there is a *Dryas* mat behind the patchwork quilt, and this mat becomes gradually poorer as it changes into the sparse community of the plateau behind, often passing through a fjaeldmark stage like that listed above for dry cliff-tops, though the flora is poorer.

An example of typical *Dryas* mat with willows was listed near the cliff-top in one of the less luxuriantly vegetated regions without a patchwork quilt, but where the dependence on birds was nevertheless apparent. Though it is much less retentive of water than the mossy communities, and dry at this season, the vegetation is everywhere completely closed and almost flat, having below it a soft, dark brown humous soil of pH 6.0-6.5.

ANGIOSPERMS

<i>Dryas integrifolia</i> Vahl	d.	<i>Astragalus alpinus</i> L.	o.
<i>Salix arctica</i> Pall.	a.	<i>Oxytropis podocarpus</i> A. Gray	o.
<i>Poa rigens</i> Hartm.	a.	<i>Carex misandra</i> R.Br.	r.
<i>Polygonum viviparum</i> L.	l.a.	<i>C. membranopacta</i> L. H. Bail.	r.
<i>Saxifraga tricuspidata</i> Rottb.	l.a.	<i>Luzula arctica</i> Blytt.	r.
<i>Salix reticulata</i> L.	f.	<i>Alsine Rossii</i> (R.Br.) Fenzl	r.
<i>S. reticulata</i> × <i>herbacea</i>		<i>Cerastium alpinum</i> L.	v.r.
<i>Pedicularis</i> sp.	l.f.	<i>Stellaria longipes</i> Goldie	v.r.
<i>Saxifraga oppositifolia</i> L.	o.	<i>Pedicularis lanata</i> Pall. ex Stev.	v.r.
<i>Silene acaulis</i> L.	o.		

In spite of the fact that they may in places help to bind the mat together mosses are generally little in evidence, but lichens form conspicuous grey patches, though most of those listed are relatively unimportant.

MUSCI

<i>Orthothecium chryseum</i> Schwaegr.	<i>Aulacomnium turgidum</i> Schwaegr.
<i>Tortula ruralis</i> Ehrh.	

LICHENS

<i>Ochrolechia tartarea</i> Massal.	a.	<i>C. mitis</i> Sandst.
<i>Stereocaulon alpinum</i> Laur.	a.	<i>C. pyxidata</i> Hoffm. var.
<i>Cetraria nivalis</i> Ach.	f.	<i>Alectoria divergens</i> Nyl.
<i>C. cucullata</i> Ach.		<i>Physcia muscigena</i> Nyl.
<i>C. islandica</i> Ach. var. <i>tenuifolia</i>		<i>Thamnolia</i> (Ceranina) <i>vermicularis</i>
(<i>crispa</i>) Wain.		<i>S. F. Gray</i>
<i>Cladonia amaurocrea</i> Schaer.		

XI. FRESH-WATER HABITATS.

The fresh-water habitats on Akpatok are numerous but generally of rather uncertain duration. As seen in August they are best classified as follows:

(a) Standing pools:

- (1) Dried up bed.
- (2) Temporary tarn—shallow.
- (3) Permanent lake.

(b) Running streams:

- (1) Dried up.
- (2) Occasional appearance with pools.
- (3) Free running all the growing season.

The marginal zonation of standing pools has already been described in Section VI of Part I ((4), p. 381), together with the rather similar boggy dips.

(a) *Standing pools.*

Small lakes and pools of water are very numerous over most parts of the plateau, sometimes where there is hardly any appreciable valley. They seem rarely if ever to be very deep, and generally they are quite shallow, so that even when they are 300 or 400 yards across they can often be waded through with fair ease.

(1) *Dried up bed.*

The tarns which dry out completely in summer generally seem to lose most of their water through a run-off hole (see VII (a) in Part I, (4), p. 383), for there still remain many much shallower ones which even at a late season have had their water level but little reduced by evaporation. Size and duration of the tarns vary greatly, as does the rate of drying up of the bed when the water has left it. An example of a frequent type that probably remains damp throughout the summer has been described above (see VII (a), Part I, (4), p. 384). This had marginal communities of *Pleuropogon Sabinei* (Soland.) R.Br., while longer-lasting examples may contain sedges and even cotton-grasses. Below come regions of drying bed which may be fairly well colonised, but further down the zones become poorer and poorer, if they are marked at all, until the centre near the run-off hole, where the water left it latest is almost completely barren. Where the tarn is small but of this deep-centred form, the sides, sloping towards the run-off hole, may be almost of the "flowing earth" type and entirely barren, especially where there is a long-lasting supply of ground water. When dry they may remain barren, or be colonised by *Deschampsia alpina* (L.) Roem. and Schult. and sometimes by a few seedlings of *Cardamine*. The best vegetated beds are often those of very shallow tarns, or flooded areas often of considerable extent, which had never been anywhere more than a foot or two deep, and which had soon dried off to leave bare areas for colonisation probably quite early in the season, for there is no lasting

supply of water. In one example there were scattered flat stones which were quite bare, for like the bed of a rocky watercourse they dry off immediately the water has left them, but the rest of the bed was mostly of dry cracking mud extensively colonised by *Deschampsia alpina*. This grass in places almost covered the ground with its rosettes, from which grew tall slender flowering axes, but no other species even of lower plants were to be found.

(2) *Temporary tarns.*

There are many pools which, though shallow, still contain water in the middle of August, but whose water-level has receded considerably. Such slow loss of water may follow late thawing of the ground and be due to seepage through joints in the limestone substratum, but is probably due in part also to evaporation where this is not made good by inflow from percolation or melting snow, for precipitation in the summer of 1931 was very small. The margin of the tarn may be of plateau polygon communities or more barren limestone, or, if the area is flat and tending to marshiness, there may be communities of the type indicated in VI (b) (Part I, (4)). The dry or still damp zone left by the late recession of the water is, however, almost always quite barren, though darkened by a silty or diatomaceous deposit. It is left too late for colonisation by higher plants, and since the tarn probably dries out completely before the end of the summer it is generally devoid of multicellular algae.

Some more permanent examples which recede but little in level, especially where the bed is of mixed stones and mud, may support in shallow parts near the margin a thick tangle of a moss, probably *Drepanocladus exannulatus* Warnst. var. *brachydietyus* (Rem.) Grout., brown with diatoms, and this may be left stranded on the sides when the water has left them. A species of water crowfoot, though a rare plant on the island, occurs towards the margin of some of the lakes, and in one or two instances was also found stranded on the mud when the water had receded.

(3) *Permanent lakes.*

The small pools fed by melting snow patches, which in some cases at least are permanent, may have the water at their margins thick with filamentous green algae (see Part I (4), pp. 390-391, and Pl. XXXIX, phot. 36). The larger permanent lakes, which are so numerous in almost all parts of the island, are often much less vegetated, though their margins may support a lush cotton-grass or *Carex* bog. Pl. XXXVI, phot. 30 (Part I (4)), shows a small and very shallow lake bounded on one side by such a bog, though on the other it is relatively barren. The lake itself contained no higher plants or even multicellular algae, and the same is true of many larger lakes of undoubted permanency, whether the bed be of rocks, stones or mud. Sometimes, near the margin, there occurs a more or less floating community of *Pleuropogon Sabinei* or more rarely of "*Ranunculus aquatilis*," but in most cases the surfaces of the larger lakes are liable to be so animated by gales that no such

communities can develop, and there is a sharp line between the water and its marginal community or barren, wave-washed edge. Thus the lake in Pl. XXX, phot. 11 (Part I (4)), is in an exposed situation and has its shores entirely barren, though the water-level has fallen but little during the summer (the fall is indicated by the dark margin, and more exactly by the boulder in the water); but a smaller pool in a sheltered valley in the south had a magnificent marginal community of *Eriophorum polystachion* L. growing out into the water but with axes still rising a foot above the surface, and approaching the "reed-swamp" type. In this case the *Eriophorum* seemed really to be aggressive, filling up the lake by depositing humus and collecting the silt brought in by a stream, so that it could soon be followed by the marginal zones described in VI (a) (Part I (4)). There is no *Sphagnum* on the island, and in this case no moss to help in the aquatic stages of the hydrosere, but in some lakes an aquatic moss of rank growth forms a tangled investment over the bed at the margin.

Still more exceptional in its vegetation is another lake situated in a large and relatively sheltered valley towards the north end of the island¹, where although there is no outlet stream or ravine the water-level is kept fairly constant by swallow holes round the margin. The water is in most places no more than a foot deep near the margin, with a muddy bottom from which grow hummocks of dark humous material accumulated largely by the growth of *Eriophorum* spp. (both *E. polystachion* and *E. Scheuchzeri* are abundant) which still dominate the smaller tussocks and the damper edges of any larger boggy areas. These damper edges are soft, and the feet may sink into them many inches, but the centres are raised and much drier, with a mixed grassy vegetation (see Part I (4), p. 382) which is apparently favoured by the White-rumped Sandpipers and other small waders (and perhaps sometimes larger wildfowl) which visit the lake (see (9) pp. 169 and 202): the abundance of their droppings may also have affected the aquatic communities. In some places the pools were being colonised by non-flowering cotton-grass, in others by pure families of *Pleuropogon* whose leaves formed a floating mat on the surface of the water. Where a streamlet entered a pool there was an abundance of *Ranunculus hyperboreus* Rottb. and some *Equisetum variegatum* and *Carex membranopacta*, all growing in the water. Other plants growing in the water hereabouts were *Carex rariflora* (Wahl.) Sm., mosses—which sometimes formed tussocks at the edges of the humous hummocks and included *Hypnum* sp. (near *molle*)—filamentous green algae, and gelatinous Cyanophyceae—also in places a brownish deposit, probably of diatoms.

(b) *Running streams.*

These must be numerous after the thaw in early summer, but by the end of August the majority have dried up completely: others, in sheltered ravines rather than the shallower beds, may have stopped flowing but have left a

¹ See plate facing p. 170 in *The Isle of Auks* (9).

trail of pools; while others again are free-running and more or less permanent, either because they drain a large area or because they have a surer supply of water from a spring or a patch of melting snow. The more rocky or bouldery the bed the more barren it is, whether the stream is permanent or dried up.

(1) *Dried up.*

The beds of dried-up streams are generally formed of boulders and entirely barren¹. Thus it is rarely that any form of plant life is to be found in the dried stream beds in the narrower ravines, where there is a great rush of water in early summer; but in more open, shallow beds whose stream of water is less torrential and varies less in height at different seasons or in different years, there may be marginal "beaches" supporting sometimes a closed community of higher plants—see Pl. XXIX, Phot. 7 in Part I (4). Where the stream has been slow enough for the deposition of silt in eddies, there may be a few small moss tussocks even in the middle of the bed, though in most places this is of limestone boulders washed clean and white. The plants of the dry marginal "beaches" and silt cones, and the more casual ones in other dried-up parts of the bed, are described below, from a stream which was still running in the centre and presumably lasted throughout the growing season.

A very different appearance is given by shallow ditches in sheltered positions on the plateau. They presumably support only a slow stream of water in early summer, and so their surface is of dried mud darkened by humus from the tiny bushes of *Salix herbacea* which colonise it, often thickly, though without the aid of any other plants.

(2) *Occasional appearance with pools.*

The porosity and solubility of limestone and the usual bouldery nature of the bed must frequently contribute to the disappearance of the stream from the surface long before the flow has actually ceased. The stream continues underground, becoming visible above ground, though in reduced volume, wherever the bed is impervious. In other cases occasional pools may remain along the course of the stream. Generally such intermittent or transient aquatic habitats are devoid of any macroscopic plants, though in some cases a few filamentous green algae may occur.

(3) *Free running throughout the growing season.*

Such streams as are still running in the middle of September are generally greatly reduced in size, and may show zones due to the gradual recession of the water-level. The zones are best seen where the bed is broad and open, but even then may be only poorly marked. The slopes beyond the margin may be almost barren, or bear one of the usual valley-side communities. In places large streams may have at their margins silty or gravelly "beaches" whose

¹ A good example is seen in the plate facing p. 118 in *The Isle of Auks* (9).

flat surfaces may support anything up to a closed community of mixed *Salices*, *Dryas*, grasses, *Saxifragae* and other plateau-land plants.

Below comes the bed of the stream (Pl. XVII, phot. 2), whose dry marginal zone is less depressed and at a level probably only washed at the time of the melting of the snow in early summer. Among its rocks and boulders are small cones of sandy material, often damp below the surface. It was principally on these that the following colonists occurred in one example, forming near the margin of the bed a sparse open community in which *Salix arctica* was the biggest and most conspicuous plant, in places quite frequent:

<i>Salix arctica</i> Pall.	f.	<i>Puccinellia angustata</i> (R.Br.)	r.
<i>Saxifraga oppositifolia</i> L.	o.	Rand and Redf.	
<i>Polygonum viviparum</i> L.	o.	<i>Cerastium alpinum</i> L.	r.
<i>Equisetum variegatum</i> Schl.	r.	<i>Alsine Rossii</i> (R.Br.) Fenzl	v.r. (1)
<i>Poa alpina</i> L.	r.	<i>Dryas integrifolia</i> Vahl (seedling)	v.r. (1)
		<i>Draba Bellii</i> Holm.	

This zone seemed in most places to be devoid of lichens, but the following mosses occurred as small tussocks, either in niches in the larger boulders, or on the cones of sand where they were sheltered behind boulders and remained damp:

<i>Bryum pendulum</i> Schp.	<i>Hypnum scorpioides</i> L.
<i>Drepanocladus vernicosus</i> (Lindb.) Warnst.	<i>H. stellatum</i> Schreb.

In the zone below, though occasional tufts of moss may persist, the bed is almost barren: near the water it consists of boulders entirely devoid of any form of plant life and probably freed from fast-rushing water only late in the summer when they can dry off immediately.

The streams themselves in these more open plateau situations are less disturbed and less subject to rapid fluctuations in height than those in ravines nearer the sea, though the bed may be rocky and the current rapid even when the water is low. In the more open places with a slow current the surfaces of the rocks in one example were green with filamentous algae, and their sides brown with an investment whose nature was not determined, but which probably consisted in the main of *Schizonema* sp., as did some other deposits of this nature. Where the water ran faster, the bed had a greenish investment of the Chroococcaceous *Aphanocapsa* sp. near *littoralis* Hansg.

A different type of stream, met with more rarely on the plateau, flows from some lasting supply of water such as a large lake, spring, or snow patch, and varies but little in height throughout the growing season. The current is sluggish, with a dark muddy bed and lush marginal communities of sedges, cotton-grass or grasses in which bushes of *Salix* may grow, while in a still more luxuriant example, before it flowed into a small lake in a sheltered valley towards the south end of the island, the bed was deep and marshy, with peaty banks formed by the growth of mosses. Behind came the lush bog described in Part I (4) on pp. 381-382.

XII. MARINE HABITATS.

(a) *Brackish water lagoon.*

The only lagoon discovered on the island fills the base of the gap in the cliffs known as Harp Cove, and is seen in Pl. XVIII, phot. 5, taken at low spring tide. It is separated from the sea by broad banks of shingle through, or sometimes over, which the water comes or goes according to the tide. It is small, being nowhere more than 4 ft. deep when, as at the time the photograph was taken, most of the water has filtered out at low spring tide. At such times the bed of the lagoon is left far above the level of the sea, for the tide range in Ungava Bay is very considerable (see p. 187). At high spring tide the lagoon fills up with water which has almost the full salt content of the sea except at the upper end where a stream of fresh water flows into it. This stream is the second largest on the island, and makes the water of the upper end of the lagoon near its mouth almost completely fresh at low tide, especially during the melting of the snow in early summer, when it must carry a much greater rush of water.

To estimate the changing salinity of the water, samples were taken at hourly intervals throughout the rise and fall of a spring tide in early September. The samples were taken at one point near the upper end of the lagoon not far below the place of entry of the stream. The mistake was made of taking the samples always from near the surface of the water instead of at a definite depth from the bottom—the mixing of such slow streams of relatively fresh and salt water exhibits complicated phenomena due to their respective densities which vary with salt content and temperature, while here conditions must also vary with the different tides and the season of the year. Probably in this case there was a tendency towards spreading of the warmer fresh water over the surface (the very level at which it entered the lagoon), so that the samples would give a smaller salt content than that actually existing at the bottom—except at low tide just near the stream, where the water is probably all quite fresh. Nevertheless, the fact that mixing is rapid was indicated by the appearance as the salt water entered of “curly wiggles” near the surface, and the following table of the salt content¹ as indicated by titration with silver

Time	Remarks on height of tide, etc.	Percentage of chloride, sea water = 100 %
A.M. 9.40	Tide rising but water still draining out of lagoon	1.24
10.40	Lagoon rising, sea water entering through shingle bar	57.3
11.40	” ”	86.5
P.M. 12.40	Sea water pouring over bar	90.9
1.40	Sea and lagoon continuous	84.9 (?)
2.40	Tide high, already turning	97.7
3.40 }	Tide and lagoon surface falling	{ 88.1
4.40 }		{ 84.5
6.40 }		{ 30.8
7.40	Tide almost low	6.86
8.40	Tide low or beginning to rise	1.8

¹ For these analyses I have to thank my brother **Oleg Polunin**, of Magdalen College, Oxford.

nitrate may be worth giving: at least it shows that towards its upper end the water of the lagoon may range from almost the full salinity of the sea to fresh water containing hardly any chloride.

The tail end of the lagoon, where the water is always fairly salt, has a bed of rounded stones covered with *Pylaiella littoralis* (L.) Kjellm. dark brown with diatoms. There are occasional bright green tufts of *Cladophora* sp. growing on some of the larger boulders, and in places between the stones are small muddy deposits (of diatoms?).

The banks above (see Pl. XVIII, phot. 5), exposed at low tide but covered with salt water at high tide, have their stones green with *Urospora penicilliformis* (Roth.) Aresch. Higher up this is confined to the under sides of the stones which remain almost continuously damp. The only other species appearing here is a *Cladophora*.

That the luxuriant covering of *Pylaiella* depends on the salt in the water is indicated by the barrenness of pools, which, as soon as they are left by the tide, are filled with fresh-water seepage from the cliffs. On the other hand *Urospora penicilliformis* seems tolerant of fresh water, demanding only a stable surface on which to grow, for at the upper end of the lagoon where the water is largely fresh from the stream this species clothes the stony bed with a luxuriant investment which may be rendered brownish by a great abundance of diatoms. Here again there are occasional bright green tufts of *Cladophora* sp., while the boulders by the margin and up to what is probably the high-water mark of ordinary spring tides, have their damp shaded sides a dirty green with *Urospora penicilliformis*. Above this the rocks are bare; but the stream supports *Urospora* as long as it is reached by the salt water of the highest tides. The *Urospora* growing on the bed in deeper places is brown with naviculoid diatoms, chiefly very abundant *Schizonema* sp.

The cliff behind has its perpendicular face hung with green festoons of *Enteromorpha* sp., which in places cover the surface, though they become thinner towards the level of the very highest tides. Even below this level, on the more stable shingle banks, very occasional specimens of *Phippsia algida* (Soland.) R.Br. and *Puccinellia angustata* (R.Br.) Rand and Redf. may occur, growing in such a position that they are temporarily submerged by the very highest tides.

(b) Salt water.

(1) Recent shingle of the seashore.

The manner in which great perpendicular cliffs rise sheer from a limestone shelf running almost all the way round the island has been described in the Introduction (4). Nevertheless at many points shingle collects in the angle between shelf and cliff base (see Pl. XVIII, phot. 6¹), and where a break occurs in the shelf opposite the mouths of some of the ravines there are extensive shingle beds, as around the lagoon at the point named "Harp Cove."

¹ And for better examples Pls. XXVII, phot. 3 and XXVIII, phot. 5, in Part I (4).

The pebbles and small boulders comprising these beds of recent shingle are almost all of limestone, though a few erratics are generally to be found. The beds are as a rule rather steep, heaped up by the frequent storms, and while those which are lower and more dynamic are entirely devoid of vegetation, being submerged by spring tides, the ones above the marks of the highest tides are doubtless knocked about and often completely rearranged by the waves and wind of storms. The vegetation of this zone is extremely sparse—often no vestige of plant life can be found over areas of many square metres, while in others it is confined to very occasional patches of yellow crustaceous *Caloplaca murorum* Th. Fr. growing on some of the larger boulders.

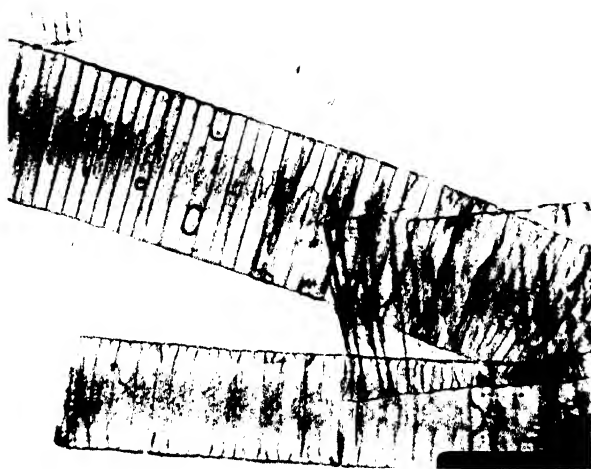
In flatter, less disturbed areas at the tops of the highest shingle slopes there is a sparse open community of the following angiosperms, whose aggregate in a given area is generally no more than f.

<i>Cerastium alpinum</i> L.	o.-l.f.	<i>Alsine Rossii</i> (R.Br.) Fenzl	r.
<i>Lychnis apetala</i> L.	o.	<i>Festuca brachyphylla</i> J. A. and	r.
<i>Puccinellia vaginata</i> (Lange)	o.	J. H. Schult.	
Fernald and Weatherby		<i>Cochlearia groenlandica</i> L.?	v.r. (1)
<i>P. angustata</i> (R.Br.) Rand and Redf.	r.-o.	(dwarfed seedling)	
<i>Ammodeinia</i> (<i>Arenaria</i>) <i>peploides</i>	r.-o.	<i>Arabis alpina</i> L.	v.r. (1)
(L.) Rupr.			

That the difficulties of colonisation are increased by water deficiency resulting from porosity and the absence of a true soil is indicated by the great fibrous root systems developed by the colonists—particularly the grasses—and by the absence of mosses.

The bases of the cliffs round the island are almost all wave-washed, and where the shingle banks are extensive and high enough to support any vegetation cliffs are rare, the top shingle banks merging into rough slopes at the mouths of coves or ravines. These slopes may support an open community of the type listed for the poorer, dry valley slopes described in V (*b*) (Part I (4)), while in other places they are still rougher, consisting of great jagged blocks of limestone alternating with beds of small splinters and tiny patches of soil, whose only plants are a few grasses.

The shores of the lagoon at Harp Cove offer more sheltered areas of shingle, little if at all disturbed by storms, the banks being in one continuous slight slope. Here the driftline of decaying seaweeds is much better marked, and even below it grow occasional tufts of grass, which at one particularly high spring tide were observed to be submerged at least 2 ft. below the surface of the water. In one place, well above the reach of the highest tide, was a dip between the rising rough slope and the back of the shingle bank, which here had presumably been piled up by some exceptional storm that had washed strongly even into the back of the cove. The bed of the dip was of small shingle, with some finer soil and humus more retentive of water, so that it supported a community, in places half-closed, which gave the following list:



Phot. 8. *Fragilaria islandica* (highly magnified) (p. 188).



Phot. 9. *Licmophora Lyngbyei* in valve and riddle view; also *Fragilaria islandica* epiphytic on *Cladophora* (highly magnified) (p. 188).



Phot. 10. *Parafavella* sp. by the side of *Rhizosolenia styliformis* (highly magnified) (p. 190).

POLUNIN—AKPATOK ISLAND

<i>Puccinellia vaginata</i> (Lange)	a.-d.	<i>Puccinellia angustata</i> (R.Br.)	o.
Fernald and Weatherby		Rand and Redf.	
<i>Cerastium alpinum</i> L.	f.-a.	<i>Cochlearia groenlandica</i> L.?	o.
<i>Ammodenia</i> (<i>Arenaria</i>) <i>peploides</i>	o.	seedlings	
(L.) Rupr. (big tussocks)		<i>Salix arctica</i> Pall.	r.

Moss:

Bryum calophyllum R.Br. (or near) a., s.-d

(2) *Intertidal zone.*

The coasts of Akpatok are extremely exposed, there being few bays or extensive reefs to afford shelter from storms. In places the actual shore is formed by the shingle banks described above, and where these lie between the ordinary tide-marks they are absolutely barren, for the weather is rarely quiet. More often there is merely a small bank of shingle at the base of the cliff, and from its lower end a flat or terraced limestone shelf (Part I (4), see Pl. XXVII, photos. 1, 3, and also this Part, Pl. XVIII, phot. 6) runs a hundred yards or more out to sea. This shelf is in many places exposed only by spring tides, but even the neaps at high water generally reach the bases of the perpendicular cliffs, which are thus worn smooth and may be undermined by wave action, as can be seen in Pl. XVIII, phot. 7.

The more the limestone shelf is terraced down or broken the more shelter it affords for vegetation, though the flora is always very meagre. In Pl. XVIII, phot. 6, it is mostly flat, uniformly wave-washed, and hence almost barren except in the more sheltered pools. In Pl. XVIII, phot. 7, is shown a part where the shelf is broken by steps going down to the low spring tide-mark, and thus are afforded numerous sheltered corners and still more favourable pools in which algae can grow.

The spring range is about 31 ft. and the neap range about 12 ft., but a transect survey from the high to the low spring tide-marks by Harp Cove showed that the zonation is very poorly marked, except as regards growth. This is better towards the lower levels, for grinding by ice and storms keeps the rock smooth-worn and bare, so that it quickly dries off in good weather when the tide has left it. Even towards low-tide mark the vegetation is almost confined to pools or sheltered corners and crannies which do not dry off.

The wave-washed cliff base, which is submerged at least during high spring tide, is generally smooth and barren, but in niches which are sheltered and remain damp there may be an investment of *Cladophora arcta* (Dillw.) Kütz. and *Pylaiella littoralis* (L.) Kjellm.

Below, in the angle between the cliff and the limestone shelf, is a bank of shingle littered with occasional large algae detached during bad weather from the bed of the sea below low-tide mark. The bank is small, but extends through most of the range of the ordinary neap tides. It is devoid of any plant life, as is the upper edge of the limestone shelf extending from its base. On the other hand, where shallow pools occupy depressions in the shelf, though they afford no shelter for larger algae, the rock surface may be largely covered by

small brown tufts of colonial diatoms, chiefly *Fragilaria islandica* (Pl. XIX, phot. 8) and bright green ones of *Cladophora* sp. (Pl. XIX, phot. 9). The relative importance of the different diatoms in this community may be seen by adding the frequency values (p. 189) given by Mr Hendey from two samples:

12 <i>Fragilaria islandica</i> Grun.	4 <i>Rhabdonema arcuatum</i> var. <i>ventricosum</i> Cl.
10 <i>Licmophora Lyngbyei</i> (Ehr.) K. and C.	4 <i>Schizonema</i> sp.
7 <i>Rhabdonema adriaticum</i> Kütz.	1 <i>Biddulphia arctica</i> (Bright.) Boyer

Lower down, the shelf is only exposed during spring tides, and the rock surface of damper crevices may support a crumbling investment of the Rivulariaceae *Calothrix scopulorum* Born. and Flah. More often it is smooth and bare of any plants, consisting of limestone whose light colour is only broken by the pools. These are formed by flaking away of the limestone and so are generally shallow and flat-bottomed, affording little shelter for larger seaweeds; but they are nevertheless darkened by tufts of filamentous and other brown algae which may half-cover the submerged rock surface (especially at the more sheltered edges and angles of the pools), and which line any crack in the rock. The little green tufts of *Cladophora* sp. are less frequent than in the pools higher up, but a *Fucus* manages to grow in sheltered corners and cracks, though it is reduced to close-growing tufts of fronds no more than 4 in. long, and often much less.

Pylaiella littoralis (L.) Kjellm.
Chordaria flagelliformis (Muell.) Ag.
Scytosiphon Lomentaria (Lyngb.) Endl.

Cladophora sp.
Fucus inflatus L. forma (and probably type)

Pools still lower down, near the low spring-tide mark, have a dark, closed community composed of these same types except that the small *Cladophora* is replaced by a larger form (*C. rupestris* (L.) Kütz.?). Growth is more luxuriant than in the higher tide pools, the *Fucus* fronds sometimes attaining a length of 7 in., though still the plant grows in the unfamiliar form of an upright tuft, probably as an annual, like most (possibly all) of the other shore algae: among these the *Chordaria* may be mentioned as a noted annual in Europe.

Even about the low-tide mark the rocks are smooth and bare, being washed by heavy seas in summer and ground by ice in winter, so that no Laminarians or other algae more massive than the Fuci are to be seen from the shore. But any slight depression in the surface of the rock is here almost black with *Calothrix scopulorum*, on which higher types have sometimes attained ecesis, while the courses of streams of salt water from the pools are marked in sheltered angles of rock by a soft brown growth of the lower Phaeophyceae already mentioned. In this are occasional tufts of *Cladophora*, and *Fucus vesiculosus* growing more luxuriantly than the other forms, and as hanging fronds instead of upright tufts.

Where a small stream of fresh water from a cascade over the cliff pours on to the limestone shelf, its course is marked by a green closed community dominated by *Microspora* sp. Lower down it enters a tide pool and the rock

beneath the gentle flow of water of varying salinity is green with *Cladophora* sp. and *Urospora penicilliformis* (Roth.) Aresch., dotted with brown tufts of *Pylaiella littoralis*.

(3) *Marine plankton and benthos.*

The phytoplankton was collected from a row-boat in a boulding-silk net of the finest mesh obtainable, and kindly lent by the Discovery Committee. This collecting was done towards the end of August, the material being killed and bottled in formalin, though one sample from each type of haul was preserved in spirit in the hope of keeping identifiable some specimens of the more weakly siliceous diatoms and flagellates. An attempt to preserve the naked flagellates for identification in Gran's fluid was entirely unsuccessful.

The collections were made within about a mile and a half of the coast off Harp Cove on the east side of the island. Horizontal tows just below the surface were first made, then horizontal tows at 9-12.7 metres, and finally vertical hauls through about 31 metres, a depth of the order of the deepest soundings recorded. From each type of haul were taken an alcohol and three formalin-preserved samples. All present the appearance of a rich and typically pelagic diatom flora, while associated are various Dinoflagellata, with *Ceratium arcticum* very frequent.

In his report Mr Hendey indicates the frequency of occurrence of the various species after the manner adopted by Mangin in his *Phytoplancton de l'Antarctique*¹, with some modification, viz.:

Index	Frequency-degree	Number of individuals in one drop of the material
1	Very rare	1- 2
2	Rare	3- 5
3	Occasional	6- 20
4	Frequent	21- 30
5	Abundant	31- 50
6	Very abundant	51-100 or more

As an indication of density in the sea these numbers are purely relative. Each horizontal haul occupied 20 min. and presumably all the planktonic matter in the volume of water actually passing through the net during that time was concentrated in the bottle and preserved, though the amount would depend on speed, etc. The individuals in a drop of the sample fluid thus represent an enormous concentration, and the number given refers to this increased density.

As is only to be expected, there is little difference between the surface and the 9-12.7 metre lots, both flora and frequencies being very similar, which suggests that the density of most species varies little between these narrow limits of depth. In the case of the vertical hauls an attempt was made at correlation with these results by concentrating into each sample the yield

¹ 1915.

from four separate vertical hauls from the bottom, for each of these took about 5 min. if the net was hauled at about the same rate as the boat moved when towing. In this case there is a difference from the vertical hauls and it may be significant, the main suggestion being that the discoid forms are less abundant towards the bottom, while the same applies to some species of *Chaetoceros*.

The other types are given much the same frequency numbers as in the samples from the horizontal tows, and must be either uniformly abundant throughout the 31 metres or else especially concentrated at some level from which horizontal hauls were not taken.

On the whole, however, the analysis shows little difference between the various samples, and the frequency numbers need hardly be published. In the list given below, the numbers assigned to a species in the twelve different samples have all been added together, so as to give an idea of the relative importance of each species in the plankton flora.

The almost entire absence of resting spores indicates that the samples were taken towards the end of the summer of the region. There is rarely any indication of auxospore formation, though one very interesting case was discovered in *Leptocylindrus danicus* Cleve, where the auxospore was developed from the girdle portion of the cell at right angles to its main axis.

Apart from *Chaetoceros*, biddulphioid diatoms are poorly represented; one form, however, which only occurred once, viz. *Isthmia nervosa* Kütz., has not been recorded from these regions before¹.

The nomenclature followed is that of Lebour in *Planktonic Diatoms of Northern Seas*:

- | | |
|--|--|
| 52 <i>Chaetoceros debilis</i> Cleve | 11 <i>Chaetoceros compressus</i> Lauder. |
| 50 <i>Thalassiosira Nordenskiöldii</i> Cleve | 10 <i>C. pseudocrinatus</i> Ostenf. |
| 44 <i>Chaetoceros socialis</i> Lauder. | 10 <i>C. teres</i> Cleve |
| 41 <i>Thalassiosira subtilis</i> Ostenf. | 7 <i>Melosira Borreri</i> Grev. |
| 40 <i>Chaetoceros atlanticus</i> Cleve | 7 <i>Nitzschia seriata</i> Cleve |
| 34 <i>Fragilaria islandica</i> Grun. | 6 <i>Cocconeis costata</i> Greg. |
| 33 <i>Coscinodiscus subtilis</i> Ehr. | 6 <i>Dactyliosolen antarcticus</i> Cleve |
| 28 <i>Rhizosolenia styliformis</i> Bright. | 6 <i>Eucampia zodiacus</i> Ehr. |
| 26 <i>Chaetoceros decipiens</i> Cleve | 6 <i>Rhizosolenia alata</i> Bright. |
| 23 <i>C. gracilis</i> Schuett. | 4 <i>Chaetoceros borealis</i> Bailey |
| 23 <i>Coscinodiscus radiatus</i> Ehr. | 3 <i>Leptocylindrus minimus</i> Gran |
| 22 <i>Chaetoceros constrictus</i> Gran | 2 <i>Bacteriosira fragilis</i> Gran |
| 22 <i>C. convolutus</i> Castr. | 2 <i>Chaetoceros diadema</i> Ehr. |
| 16 <i>C. fragilis</i> Meunier | 2 <i>Eucampia groenlandica</i> Cleve |
| 15 <i>Thalassiosira rotula</i> Meunier | 2 <i>Streptotheca thamensis</i> Shr. |
| 15 <i>Coscinosira polychorda</i> Gran | 2 <i>Fragilaria oceanica</i> Cleve |
| 14 <i>Thalassiosira gravida</i> Cleve | 1 <i>Chaetoceros holsaticus</i> Schuett. |
| 13 <i>Coscinodiscus excentricus</i> Ehr. | 1 <i>C. septentrionalis</i> Oestr. |
| 12 <i>Lauderia gracilis</i> Grun. | 1 <i>Biddulphia balaena</i> Ehr. |
| 12 <i>Leptocylindrus danicus</i> Cleve | 1 <i>B. arctica</i> (Bright.) Boyer |
| 12 <i>Rhabdonema adriaticum</i> Kütz. | 1 <i>Isthmia nervosa</i> Kütz. |

In some of the samples, though their occurrence is rare, are peculiar organisms having strongly marked diatom characteristics but belonging to a group of Ciliates, the Tintinnoidea. Three species of the genus *Parafavella*

¹ The reservation should however be made that the net had previously been used elsewhere!

Kof. and Camp. (*Tintinnus* Ehrenb.) of the family Cyttarocylidae are identifiable¹, viz.:

P. denticulata (Ehr.) K. and C.
P. media (Bdt.) K. and C.

P. elegans (Ost.) K. and C.

Benthos. The following notes may give some indication of the nature of the benthic vegetation.

No Laminarian fronds could be seen from the shore even at low spring tide, probably because the grinding action of ice in winter confined the algae growing there to small annual forms; but feeling with the sounding-line or cod "jigger" showed that such "oar weeds" covered the bottom at greater depths, and extended down to some 23 or 24 metres. This depth off Harp Cove was reached about half a mile from the shore, and beyond, on the deeper but still only slightly shelving bottom, there seemed to be no large fronds. The bottom here seemed to be of mud containing some larger gritty particles, for such matter stuck to the tallow at the base of the sounding-lead, which did not in the samples taken pick up any diatomaceous or other organic materials.

The chief alga seems to be *Laminaria longicuris* de la Pylaie, with fronds growing regularly to a great size. One of the larger plants cast up on the shore had the following measurements:

Total length	47 ft.
Length of stipe	18 ft.
Length of lamina	29 ft.
Greatest circumference of stipe	3½ in.
Greatest breadth of lamina	16½ in.

Other large algae floating after detachment by storms, or cast up on the beach but quite fresh, and certainly coming from the vicinity, were the following:

Laminaria digitata (L.) Lamour.
Alaria Pylaii (Bory) J. Ag.
Alaria sp. (battered fragment, might have come from the mainland?)
Agarum Turneri Post. and Rupr.

Growing attached to the larger plants of *Laminaria* are the following Rhodophyceae, all belonging to genera which are represented by epiphytic or omnicolous species around the British coasts:

<i>Pantoneura Baerii</i> (Post. and Rupr.) Kylin	<i>Rhodophyllis dichotoma</i> (Lepch.) Gobi
<i>Phycodrys rubens</i> (Huds.) Batt.	<i>Rhodymenia palmata</i> (L.) Grev.
<i>Ptilota pectinata</i> (Gunn.) Kjellm.	

CONCLUSIONS²: THE MAIN PLANT COMMUNITIES AND THEIR PROBABLE SUCCESSIONAL RELATIONSHIPS.

In the introduction it was explained (4, p. 346) how and why, for purposes of description in the general text of this contribution, the types of vegetation occurring on Akpatok would be classified physiographically according to habitat rather than ecologically according to physiognomy or floristic com-

¹ A specimen of one of them is seen alongside the *Rhizosolenia styliiformis* in Pl. XIX, phot. 10.

² The writer wishes to thank Prof. George E. Nichols of Yale University for suggestions and help in connection with the drafting of this section.

position. But in order to bring these descriptions more into line with other accounts of vegetation, it may be well in concluding to attempt to recognise the more important and easily delimitable *plant communities* seen on the island, quite apart from habitat boundaries, and finally to bring these communities into their probable places in a general successional scheme.

The open *Dryas-Salix*-herb community of the plateau polygon areas¹ of Akpatok does not represent the climatic climax of the Hudson Strait region. In fact it does not even approximate to this condition, which is apparently represented by the closed, heathy community generally developed on the adjacent mainland, but little if at all on the island. The plateau comprises, however, most of the area of the island, and thus the plateau community (since it seems to be in equilibrium with the various determining factors now obtaining) must be regarded as some sort of climax—in all probability a *sub-climax* maintained very largely (although not wholly) by unfavourable conditions of exposure, and therefore due indirectly to topography.

That local climatic and often microclimatic conditions are largely responsible for the reduction of growth, and the failure of succession to advance beyond the open *Dryas-Salix*-herb stage over most of the island, is strongly suggested by the much more luxuriant vegetation which may develop in almost any sheltered locality. But at the same time, even in the most exposed situations, relatively luxuriant vegetation tends to develop locally wherever there is a morainic deposit of acidic rocks, or any addition of nitrogenous or other food substances by nesting birds. It would seem, therefore, that the extremely impoverished character of the vegetation of the general plateau must be also influenced in high degree by peculiarities introduced by the limestone surface². This limestone causes or at least aggravates the following difficulties with which (quite apart from a rigorous climate) the plants have to contend: (1) instability of surface, (2) local aridity due to porosity, (3) lack of humus and soil acidity, and probably (4) great deficiency in combined nitrogen and perhaps in other "essential" elements. Thus the present main Akpatok type of vegetation is determined partially at least by edaphic conditions, and to indicate this and other peculiarities we may call it the "polygon sub-climax."

¹ See Part I ((4), p. 352 *et seq.*)

² In the course of a recent visit (1933) to Spitsbergen (latitude nearly 80° north in Europe) the writer was so struck with the remarkable similarity of the vegetation and flora, as well as the general aspect, of certain exposed limestone areas in the King's Bay region to those of the general plateau of Akpatok (latitude only 60° north in America) that several days were spent in careful observations which it is hoped to embody in a future paper. Such similarity, in spite of the widely different geographical positions, suggests that limestone may sometimes be the primary factor in determining the vegetation—at least until a thick deposit of humus has been accumulated. This is supported by observations made in 1934 on Southampton Island to the north of Hudson's Bay, where the areas of acidic rocks support quite luxuriant vegetation but others of pure limestone are largely barren. On the other hand the *flora* even in the Arctic is often richer on limestone areas—due in part to lack of competition and poor growth, so that bare areas are left for the eecsis of the feebler colonists.

On the other hand it must be remembered that the polygons themselves are not yet in equilibrium with the climate. Indeed if the climate remains unaltered they will probably not be in equilibrium with it until they become reduced to a homogeneous mud (see (4), p. 358). No example of this complete comminution to mud was recognised on Akpatok, and it is impossible to say just what vegetation such a surface would eventually support. The character of the vegetation, like the speed with which homogeneity can be reached, would probably depend greatly upon local water conditions. It seems most likely, however, that these areas of completely comminuted mud would tend in time to become occupied by a continuous cover of mixed sedges, grasses, forbs and willows of the type encountered towards the south-west end of the island (see pp. 162–163), where the ground is less cut up by surface drainage, and where, conditions being often more sheltered, the snow presumably lies in winter instead of being blown into the ravines. Weaver and Clements (7), p. 427) would see in some such community the probable true climatic climax of the American Arctic. But the present writer, from a cursory examination of the adjacent mainland¹ and numerous observations made elsewhere (e.g. (1, 3, 11, 12)) by others and by himself, would expect to find in the end a tendency, at least in this region, towards a more heathy and xeromorphic climax dominated by ericaceous ground-shrubs or by *Empetrum*.

Such a heathy community already occurs on Akpatok, even on the limestone, in places of sufficient shelter and humus accumulation, and while at present it occupies the position of post-climax if we consider the area of Akpatok alone², it appears to approach the true climatic climax of the adjacent mainland.

The soils and surface features of Akpatok seem remarkably immature³,

¹ Not only of Ungava Bay while on the Oxford Expedition of 1931 but quite recently of Southern Baffin Land with the Canadian Eastern Arctic Expedition of 1934.

² This is consistently done, without reference to the climate of the general Hudson Strait region or the vegetation of the adjacent mainland, in the ensuing discussion and outline of seres. It is necessary to bear this distinction in mind because with the much more rigorous conditions on Akpatok, similar grades of vegetational attainment here and on the mainland may have a very different status in relation to the climax of their particular region. Thus the closed and much mixed sedge, etc. community which appears to be the climax on Akpatok occupies on the mainland rather the position of sub-climax of the hydrosere developed there, and the open communities of polygon and fjaeldmark areas which compose the sub-climaxes at present covering most of the island would be relegated to the position of mere seral stages if we considered the Hudson Strait region as a whole. Climax vegetation is regarded as being only relatively stable—not necessarily permanent even in the face of present conditions.

³ Even the deepest of the narrow ravines dissecting the plateau are quite immature, having been produced for the most part since the last ice age. Erosion even of limestone in the Arctic is not so rapid that this does not strongly suggest some time B.C. as the probable date of the last glacial retreat on Akpatok. Moreover, archaeological work on the adjacent mainland has brought to light traces of two separate Eskimo cultures which presumably were at least several hundred years apart, although it is impossible as yet to date the earlier or Cape Dorset culture. On the other hand, Eskimo live in many coastal regions whose hinterland is still glaciated; and then again Akpatok, considering the height and exposed nature of its plateau, may have remained glaciated

and so does the vegetation. In the absence of other dominant types able to stand the rigorous conditions, the plateau remains for the most part a stony desert vegetated by the *Dryas* fjaeldmark community, or more extensively by the *Dryas-Salix*-herb polygon sub-climax community. But although in drier places there may perhaps during some seasons be such severe root competition that the intervening tracts of the polygons are physiologically closed, it is difficult to see why the plants have not taken a firmer hold at least in places where water is sufficient.

It is just conceivable that until fairly recent times the island was covered by an ice cap¹ like the not far distant south-east arm of Baffin Land, which is covered by the Grinnell Glacier down to an altitude of 1000 feet (304 metres). If this is so the vegetation may be changing and humus accumulating as quickly as the necessarily slow growth will allow. It is also possible that comminution to fine soil has become general only within comparatively recent times. But all things considered² it seems more likely that the island has been free from ice except in small patches for at least one or two thousand years³, that the general surface fairly soon reached a stage of comminution and polygon delimitation⁴ comparable with that now seen, and hence that this surface, at least where the winter snow covering is blown away, is a true desert, with ecesis so difficult and growth so limited that even to this day it is only sparsely vegetated and therefore largely lacking in humus deposits. Indeed, with the limestone almost everywhere predominant and aggravating the inhibiting effect on growth of rigorous climate and extreme exposure, there seems on Akpatok to be a fundamental (and perhaps lasting) edaphic modification of the usual primary climatic control of the vegetation of an area. Thus it seems that, not in a few places only but over almost the whole of a comparatively large island, peculiar edaphic conditions reduce growth (and perhaps favour bacterial action) to such an extent as to prevent the accumulation of humus and to make seral changes so extremely slow that the existing depauperate vegetation appears to represent a true climax.

long after the adjacent mainland was free of ice. The question of how long these mainland regions have been left free of ice is difficult and has not been agreed upon; the same must be admitted with regard to Akpatok Island.

¹ This is also suggested by the apparent immaturity of the vegetation in areas such as that shown in Pl. XVII, phot. 1, where (sometimes for no apparent reason) drastic changes occur in closely contiguous areas.

² Cf. footnote 3 on p. 193.

³ There can be little doubt that very much shorter periods of time have been sufficient for the development of closed phanerogamic vegetation in many areas farther north, for example Northern Baffin Land and North Devon Island, recently visited by the author.

⁴ When water is sufficiently abundant and comminution has proceeded far enough for their formation, the actual delimitation of stone polygons may perhaps be quite rapid; the writer has seen domed *mud* polygons formed in a single season on homogeneous alluvial deposits in Arctic Scandinavia, where they are destroyed each summer when the rivers rise with water from the melting snow.

The vegetation of Akpatok Island is therefore a very poorly developed sample of the Arctic Tundra patchwork of the Hudson Strait region, and the polygons and barrens of the exposed plateau, and the hilltops which support scarcely a plant, may well afford the poorest examples of fairly stable vegetation within this patchwork. Moreover the Akpatok plateau vegetation is itself made very patchy by even slightly different physical conditions obtaining in different places. In this part of the subarctic, conditions are so unfavourable that biotic competition is much reduced in importance and the struggle for existence is primarily with inimical habitat factors. On Akpatok these are particularly severe, so that successful established plants may remain undisturbed by other types; then in the absence of closed vegetation or of general dominance by one or two species, there results a patchwork composed of the more successful types from among the whole set of possible colonists, sometimes perhaps representing a chance distribution or at least without the locally determining factors becoming apparent. Thus the usual plateau communities appear to be of almost a pioneer type, and have probably remained substantially unaltered since an early stage in recolonisation after the final retreat of the ice.

Frequently, however, there is a change in topography producing entirely different climatic or water conditions locally. Since the general habitat factors are already so severe, even minor changes may have a profound effect upon the vegetation—most notably, as has already been mentioned, in allowing much more luxuriant or even closed vegetation, often very intricately mixed and changeable, to develop in areas that are only slightly sheltered. Finally in habitats made still more favourable by late-melting snow, by morainic deposition, or by the proximity of nesting birds, there may be a regular zonation as the ameliorating factor becomes more intense. Thus under present conditions in most areas more than one factor seems to be near the limit below which regular growth can no longer proceed, but it is only necessary to change one of the major types of factors—climatic, topographic, or edaphic—to produce locally a great improvement in the vegetation.

On the other hand, over most of the surface of the island that is not so favoured, the little growth that is made is insufficient for appreciable humus accumulation and the plants being small and stunted are quite impotent to react upon the limestone substratum sufficiently to improve the water and other habitat conditions; and hence the communities are often "migratory," or even where they appear to have the status of a climax may remain sparsely open and mixed. The limestone apparently contains insufficient silicate or other insoluble material to give a different surface as a result of leaching, and there seems little chance of an increase in food salts¹ or snow covering on most areas, or of any great amelioration of the soil unless it be connected with the further comminution of particles. It thus seems that a complete change of one

¹ It appears that nitrogen-fixing bacteria are relatively inactive in northern regions; certainly they are adversely affected by cold (8).

at least of the factors now reducing growth would be necessary before any great amelioration of the vegetation of the general plateau could take place, and that in many cases the communities are little changed from the original pioneer colonies which entered after the final ice retreat; indeed the apparently chance distribution now seen suggests just such an ordinary random colonisation.

By way of summary: the climatic, topographic and edaphic conditions on Akpatok are all very unfavourable to plant growth and have combined to keep the vegetation extremely scanty and reduced. These conditions have probably obtained much as they are to-day for at least one or two thousand years, and there is every reason to suppose that during most of this time the plant communities, being in the majority of cases too miserable to accumulate humus, have also remained substantially unaltered. Over the exposed limestone plateau which constitutes almost the whole area of the island, the vegetation is so poor as to suggest that hardly any successional advances or even marked changes (except in a few favoured localities) can have taken place since the first colonisation after the final ice retreat. Consequently it is to be presumed that the *Dryas* and other main communities now seen, although they may appear to be of almost a pioneer type, will persist at least for a very long time to come. Whether they resemble true climaxes or arrested (sub-climax) stages in an *autogenic main sere*, or merely pioneer or migratory *proseres*¹, the majority at least of these dwarf and meagre plant communities which go to make up the vegetation of Akpatok appear to be in equilibrium with the present conditions and hence relatively stable.

Nevertheless, there are sufficient apparently changing successional stages to enable the main seres to be traced. Those given below are inferred, and (with intermediate communities) cover almost the whole area of the island. There are, however, some less marked and relatively unimportant communities, several of which are described as delimited by habitat in the foregoing account, which are not mentioned here because they appear to be either purely migratory and detached, or else intermediate or deflected. The names or abbreviated descriptions of the chief distinct plant communities that were recognisable on the island in 1931 are printed in capitals in the following scheme, and after each is given in brackets a number. This number will be found in brackets and heavy type opposite the number of the page on which begins the description

¹ A *proserie* is constituted by any ephemeral (migratory) communities that are not essential parts of the true successional series which is to follow, and which is termed by Tansley (13) the "autogenic main sere." The pioneer stages of this last are able to occupy anew the initially bare surface without being dependent upon humus accumulated (or any other condition introduced) by any *proseral* stages that may have gone before.

Examples of *proseres* are the communities of grasses and sometimes woody plants which invade sand dunes and are liable to be killed by further movement of the sand before its final stabilisation by other colonists; or again, colonies of crustaceous lichens on a bare rock face over which extension may be made by higher plants rooting in crevices whether the rock face had previously been colonised or not.

of the habitat in which it occurs (see pp. 348–9 of Part I (4)), and so will act as a reference to an example of the community as far as it is described in any one place in the general text.

The following are to be distinguished:

- (1) Xerosere on limestone rock including polygons and fjaeldmark (p. 197).
- (2) Xerosere on rocky screes (p. 200).
- (3) Xerosere on well-drained sandy soils (p. 201).
- (4) Xerosere on erratic boulders and acidic soils (p. 202).
- (5) Hydrosere (?) on slopes of wet soil (p. 202).
- (6) Hydrosere in shallow lakes and pools (p. 203).
- (7) Zoned sub-climaxes of late snow (p. 207).
- (8) Zoned sub-climaxes and succession above bird-cliffs (p. 208).

I. XEROSERE ON LIMESTONE ROCK AND COMPACT SOIL OR POLYGONS RESULTING FROM ITS WEATHERING.

1a. The initial limestone rock or frost-fragmented surface may be barren or it may support a community of OCCASIONAL CRUSTACEOUS LICHENS (1). This community is developed chiefly on exposed hilltops but occurs also on disturbed areas of screes and in ravines, for lichens are certainly the pioneers on any dry rock or stone surface. On the exposed plateau of Akpatok Island such surfaces, at least where they are of limestone, are so rapidly weathered or otherwise disturbed that they can hardly ever become colonised by higher plants, so it is doubtful if the lichens are of more than proseral¹ significance. They may be a long-enduring proseral community, but do not seem to be essential to the autogenic¹ main sere, and are certainly not part of it, for the first angiosperm colonists, *Dryas*, *Salix arctica*, etc., appear on very nearly the most exposed hill-tops as soon as there is sufficient comminution to fine soil which can retain water. Such soil often shows no trace of humus between the plants. Even the larger boulders of limestone that lie scattered here and there may be almost devoid of even the smallest crustaceous lichens.

1b. The blue-green algae which may occur on the damp undersides of stones in some situations are again only proseral. These rocky fragments are never colonised by higher plants, which cannot enter the area until fine soil has been accumulated between or beneath the stones.

1c. The *SAXIFRAGA OPPOSITIFOLIA* BARRENS (2) on exposed and well-drained cliff-tops probably represent at one and the same time the pioneer and sub-climax stages of a prosera unrelated to the usual xerosere, which will proceed only when some fine soil has been made and water can be retained. Similar barrens of coarse limestone particles occur on the windswept, north-west slopes of some of the hills inland, and the dominance of binding patches of *Saxifraga oppositifolia* seems to depend on the drainage conditions and on

¹ See footnote on p. 196.

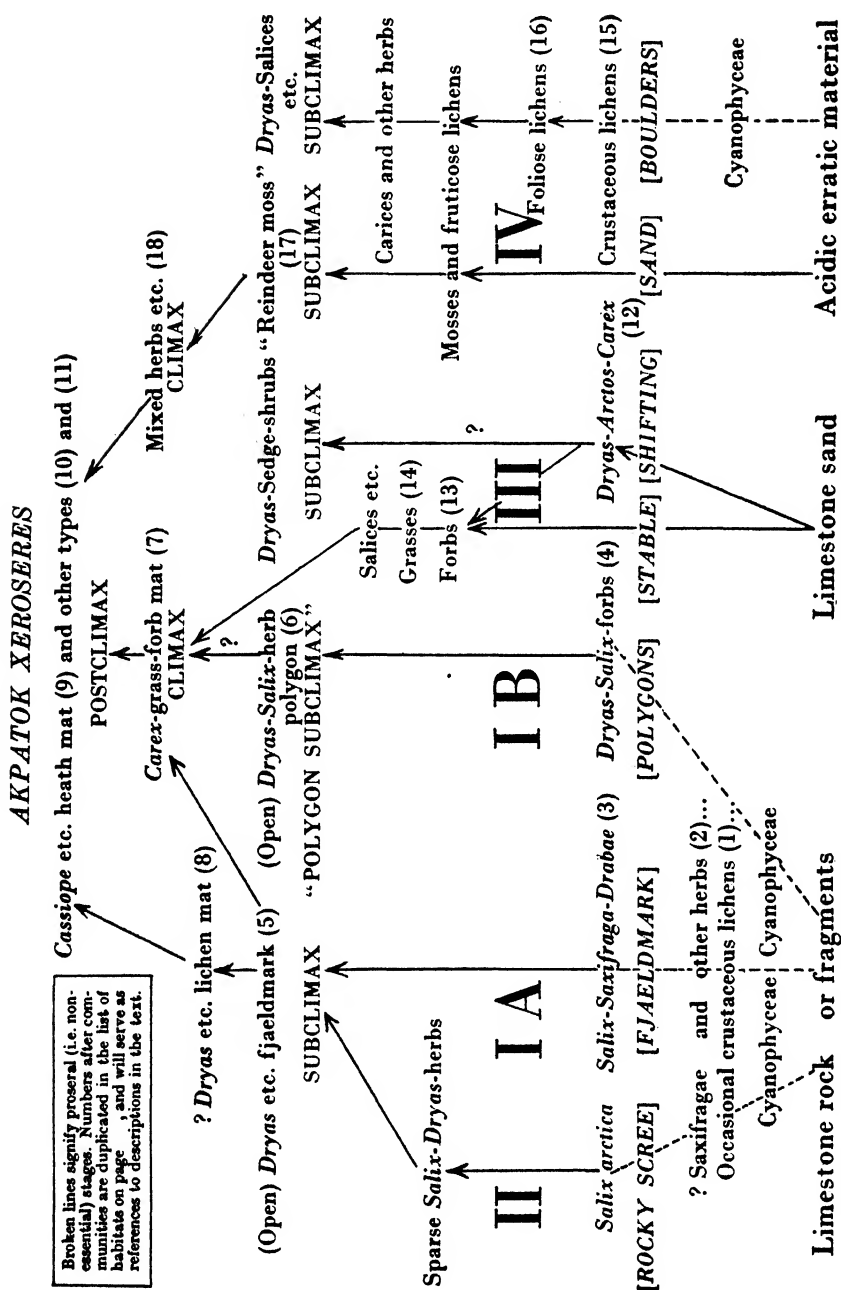


FIG. 1.

the looseness and coarse texture of the surface, so that it is unlikely to form a real stage on ordinary fjaeldmark or other areas, where large blocks still remain but some fine soil was probably made fairly quickly after the ice had gone.

One or more of these migratory communities, especially the first, probably occurred on most areas before higher vegetation gained a footing, so that they represent early stages of the whole succession even if they are not part of the autogenic main sere. The sere in the next two stages bifurcates rather clearly into "A" and "B" aspects, marked by the absence and presence, respectively, of "stone" polygons.

2A. *SALIX ARCTICA*, *SAXIFRAGA OPPOSITIFOLIA* AND *DRABA* SPP. (3), having long roots which can go down between the larger fragments to reach the soil accumulated below, are the chief colonists of heaps of fragmented rock just as they are on many of the screes proper. The same species occur, generally still more sparsely, on many rough and wind-eroded hill-tops.

2B. On flat hill-tops the surface is less dry, and, although the above are probably the first angiosperm colonists, there is now in most places a preponderance of fine soil material upon which *Dryas* can grow. Rough polygons are generally beginning to form, and although *Dryas* is the chief plant on the patches of soil, others, such as *Polygonum viviparum*, may occur; and *Salix arctica* also, but chiefly in stony places such as the intervening tracts of polygons where these are delimited. Except for one or two less reduced types the lichens are, as before, a few crustaceous forms on the larger boulders, and the angiosperms enter irrespective of them—often most successfully where there is less rock and hence less lichen growth. The angiosperms grow much better in the lee of any boulder or larger rock which gives shelter and holds snow in winter. This SPARSE IRREGULAR *DRYAS-SALIX-FORB* COMMUNITY (4), in which the plants are very widely separated, may occur extensively as a sub-climax on dry exposed plateau areas with poorly marked polygons, but is really only a poorer type of (6) below.

3A. The (open) *DRYAS*, ETC. FJAEELDMARK (5), probably to be regarded as a sub-climax, is developed on non-polygon areas including the "well-drained, poorly vegetated valley sides." The surface, consisting to a greater or lesser degree of fine soil material, is dominated by *Dryas*. This in some cases almost closes the area, but there are always a lot of bare fragments of rock lying about, and generally some still larger boulders, while in the more exposed places much even of the fine soil is left bare of plants and remains unmixed with humus, thus constituting a true and typical fjaeldmark area. Associated with the *Dryas* are *Salix arctica* (chiefly on stony, less stable areas), sedges, saxifrages, and in favourable localities often some ericaceous ground-shrubs.

3B. The *DRYAS-SALIX-HERB* POLYGON SUB-CLIMAX (6) appears to follow 2B on further comminution to soil and establishment of definite polygons. It covers most of the plateau and hence most of the island, and the terrain being stony and disturbed by more agents than one, the community is sparse and

open. Nevertheless it includes, besides the usual dominant *Dryas*, a number of rosette and other plants—especially dwarf willows, with some saxifrages and sedges, and abundant mosses in the patches of higher vegetation. The limestone fragments are still devoid of plant life except for occasional crustaceous lichens on the larger blocks or more rarely on eroded splinters, and it seems certain that there is here often practically no snow covering during the winter.

4. The climax appears to be the mixed and more or less closed *CAREX-GRASS-FORB MAT* (7), with cotton-grasses in damper places and willows in drier, which covers considerable areas towards the south-west end of the island. In places it comes to form a dense sward which probably holds a goodly covering of snow in winter, but in depressions, which presumably have a still better snow covering but nevertheless remain dry, this sward may be locally replaced by a *DRYAS, ETC.-LICHEN MAT* (8) which is directly followed by the post-climax described below. Where polygons become stabilised it seems probable that the climax is again this *CAREX-GRASS-FORB MAT* (7), for its dominants were noticed in a few cases to cover even the polygon area, which indeed on stabilisation becomes relatively well suited to their colonisation. This was in damp depressions where comminution was more advanced than elsewhere, but it is possible that in dry places which are not too exposed such stabilisation may take place before the mud stage is reached. However that may be, there is probably a complete convergence of polygon and fjaeldmark seres in the later stages, as the soil becomes more homogeneous.

5. The post-climax of both fjaeldmark and polygon types is a *CASSIOPE-VACCINIUM-RHODODENDRON MAT* (9) with or without *Dryas*, and is seen in sheltered depressions where there is a good snow covering in winter. Humus can accumulate and in the most favourable localities this community may pass to a luxuriant *EMPETRUM MAT* (10), but on the other hand in drier areas with little snow covering it thins out to a poor *CASSIOPE-LICHEN MAT* (11), generally with much *Dryas*.

II. ROCKY SCREE XEROSERE.

1. The early stages are like the fjaeldmark xerosere, with Cyanophyceae, lichens, and occasional plants of *Saxifraga oppositifolia* forming migratory proseres, often with *Draba* spp. and *Cerastium alpinum*. The higher plants grow chiefly below boulders or small rocky outcrops on the screes, where they are sheltered from the downward rush of moving particles.

2. The first real stabilisers are nearly always small prostrate bushes of *Salix arctica*, which form the nucleus of the characteristic strips of vegetation extending longitudinally down the slope. These strips include further binding tussocks of *Dryas*, saxifrages, etc., and on the less dynamic screes are able to extend, so that the surface may become progressively more stabilised, resulting in an open *DRYAS, ETC. FJAEELDMARK* (5). This is comparable with that

of poor plateau areas, except for the still greater abundance on the screes of *Salix arctica*, and the peculiar arrangement of their vegetation in strips and patches bounded by barren chutes of moving fragments of limestone, or sometimes of larger blocks.

3. With further advances of the vegetation the scree may become completely stabilised, unless water action is continually removing material from the bottom—although even this would presumably cease in time, as the gorge became more open and the slope less steep. The vegetation may remain open or become closed, but unless there is a supply of water from a spring the succession will generally proceed no further than a poor *Dryas*, etc. sub-climax, having many willows because the surface is rocky.

III. SUCCESSION ON WELL-DRAINED SANDY SOILS.

Here the communities are unimportant and of doubtful delimitation, the sequence of plant populations being determined allogenuically rather than autogenically (*i.e.* as the result of the action of external factors rather than by progressive humus accumulation and amelioration of water and other conditions consequent on the growth of plants *in situ*). However, on deposits of dry, well-drained sandy soils (although these are mostly of limestone and generally of very limited extent) there seems usually to be some sort of an autogenic sere:

1. *Elymus arenarius*, although it occurs, is rare and apparently unimportant on the island, but sandy hills inland are bound by *Dryas*, *Arctostaphylos* and *Carex nardina* (12), each of which can enter separately and form good pure patches.

2. Areas of greater stability, whether they were previously barren or had first to be bound by the above community, are colonised by abundant FORBS (13), chiefly *Epilobium latifolium* and *Polygonum viviparum*. On patches of sand deposited in sheltered ravines these herbs, with small grasses, are apparently the pioneers: mosses, although they may form a fairly complete layer beneath the dominant herbs in damper valleys, apparently only enter when the sand is bound and able to hold water.

3. GRASSES (14) quickly dominate the forbs, controlling water and other conditions on such sandy soils.

4. The turf never becomes very thick or close, and in the absence of pasturing by polar bears it seems that such areas are in time dominated by willows of good growth, except that a *Dryas*-sedge-groundshrub community persists, at least as a sub-climax, on fine soils wherever the situation is more exposed and predominantly dry.

IV. ERRATIC BOULDER AND ACIDIC SOIL SUCCESSION.

Unlike limestone boulders, erratics may be well vegetated by cryptogams, and where they accumulate a snow covering in winter may even show stages of colonisation by higher plants, although it is doubtful to what extent this may be due to manuring by ptarmigan which repair to such landmarks. The following stages may be seen, the first four generally occurring even on the most exposed plateau regions, provided the erratic boulder is of sufficient size.

1. Blue-green algae invest damp crevices but are only proseral, as crustaceous and sometimes even foliose lichens can colonise the bare rock alone.

2. CRUSTACEOUS LICHENS OF ACIDIC ROCKS (15).

3. FOLIOSE LICHENS (16).

4. Mosses and fruticose lichens, generally starting in crevices.

5. Colonisation of moss tussocks by *Carex* species, *Polygonum viviparum*, etc.

6. *Dryas* and willows enter.

The same stages may be traced on the boulders of larger morainic deposits. Here on the sheltered areas of sandy soil between the boulders, mosses seem to be the first colonists, followed by a "REINDEER MOSS" COMMUNITY (17) dominated by large fruticose lichens but still much mixed with certain tall mosses, which grow much better here than on the limestone. This community forms a thick and presumably long-enduring sub-climax, the climax proper being apparently a much mixed but CLOSED HERBACEOUS VEGETATION (18) dominated by species of *Carex* and *Luzula* and by grasses, and including patches of various forbs; also mats of such minute ground-shrubs as *Harrimanella* (*Cassiope*) *hypnoides*.

On such a morainic deposit of erratic material the area of mixed communities, although it is already very patchy, is further interrupted by post-climax patches of *Cassiope* and *Empetrum*, and in a less exposed situation would probably be covered with them. Thus it is not only the climatic factors which depauperate the vegetation on Akpatok, but also to a great extent the edaphic, so that on rocks of normal acidic tendency a heathy ground-shrub mat is the probable climax as on the mainland. On Akpatok, however, this can so rarely be developed that it has the significance rather of a post-climax, whether it is on the limestone or on the occasional morainic accumulations. On the former it can only be developed under conditions of exceptionally good shelter; on the latter it may appear in the most exposed situations, although probably some snow covering is essential.

V. SUCCESSION ON SLOPES OF WET SOIL WITH A LASTING SUPPLY OF FRESH PERCOLATING WATER.

This sere is partly determined by late-melting snow, especially in its early stages, which may be maintained as more or less persistent sub-climaxes; but there appears also to be a supply of water more lasting than in ordinary late snow areas, so that even if the snow melts early the ground remains wet in summer, and succession may proceed.

1. The first stage is generally an *OXYRIA*-SAXIFRAGE BARREN (19) which apparently may persist more or less indefinitely, especially on exposed areas or in relation to very late-melting snow. This latter condition generally prevents flowering and may have favoured a few small mosses or terricolous algae as the first pioneers in the very wettest places. These lower plants are, however, ephemeral and unnecessary—except in one or two areas over which a thick moss mat was seen to have spread, and in which the percolating water lasted presumably throughout the growing season.

2. It seems, however, that further advance in succession always depends upon the activity of mosses of tussocky growth, so that the next stage is a WET FORB-MOSS MAT (20).

3. The mat is so luxuriant in growth that considerable humus deposition must take place, and as the mosses grow up further their tops are colonised by willows, giving, at least in some examples, a *SALIX*-MOSS MAT (21). In other examples the higher vegetation is in discontinuous patches, chiefly clothing hummocks which are extending over the barren intervening depressions by the lateral growth of tussock-forming mosses, and leading to the type described as “damp, better vegetated valley sides.”

4. As the surface, especially of hummocks where these occur, becomes drier with the raising of the level as a result of the considerable humus deposition under such favourable growing conditions, it is colonised by *Dryas* and *Carex misandra*.

5. Under still more favourable conditions, at least on the more sheltered valley sides with a good snow covering in winter, the above community passes direct to a post-climax *CASSIOPE* MAT (9), generally with *Rhododendron* and much *Vaccinium*, and with *Dryas* and *Carex misandra* persisting. Sometimes there is maintained instead a *CAREX*-GRASS-FORB CLIMAX (7) or a community with more willows, but generally conditions are favourable for humus accumulation and the usual post-climax appears, or at least a *CASSIOPE*-LICHEN MAT (11).

VI. THE HYDROSERE.

As with the other seres, the stage at present reached, and often the sequence itself, depends on exposure, for many of the permanent lakes on the plateau are almost barren, even around their margins. In other cases the sere is upset by disappearance of the water, and while this may lead to the maintenance of various sub-climaxes it may presumably vary in different years and give all sorts of complex results. More broadly, the following sequence may be traced:

1. There are few macroscopic aquatic plants except FILAMENTOUS GREEN ALGAE (22) in certain pools, and in some others a large coarse unidentified moss which with other species may form a thick tangle near the margin. These and the rather rare “*Ranunculus aquatilis*” must deposit a certain amount of humus on the bed, but they only occur in some pools and cannot be very important.

The Vegetation of Akpatok Island

AKPATOK HYDROSERES

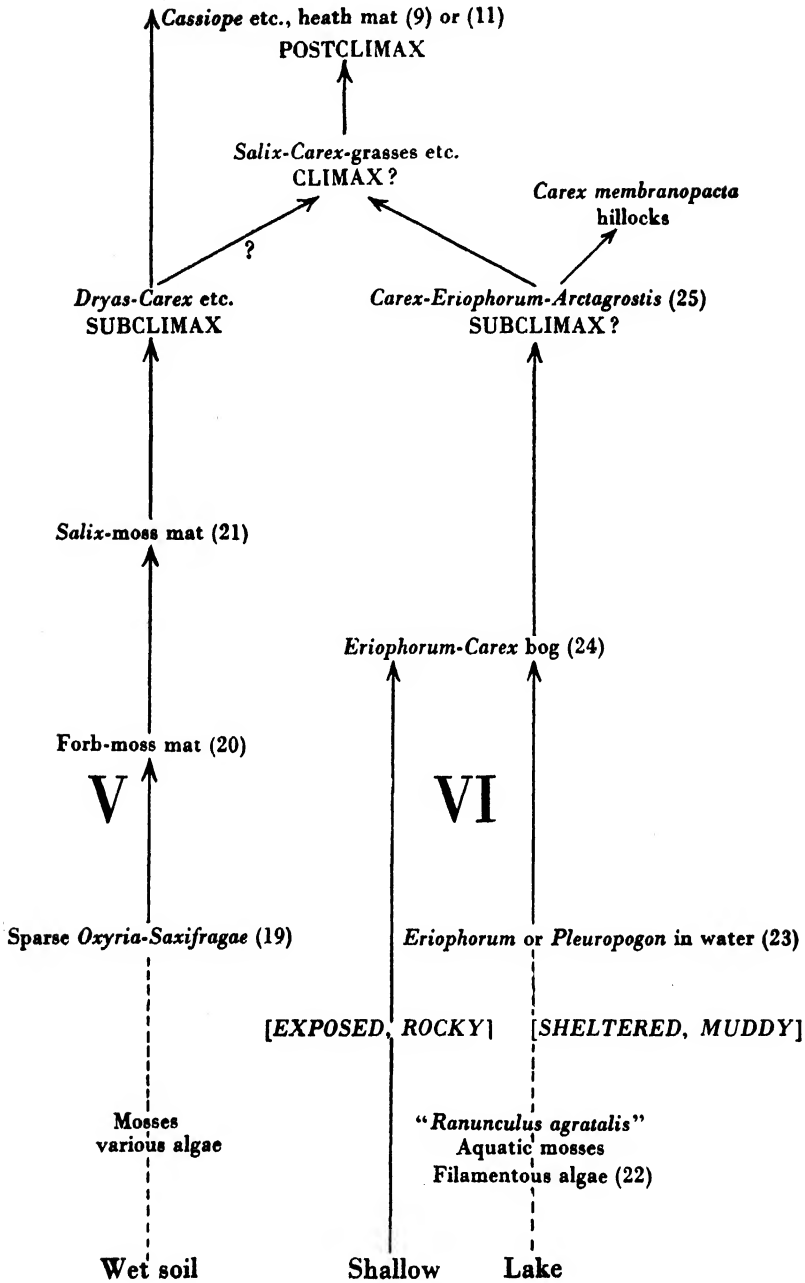


FIG. 2.

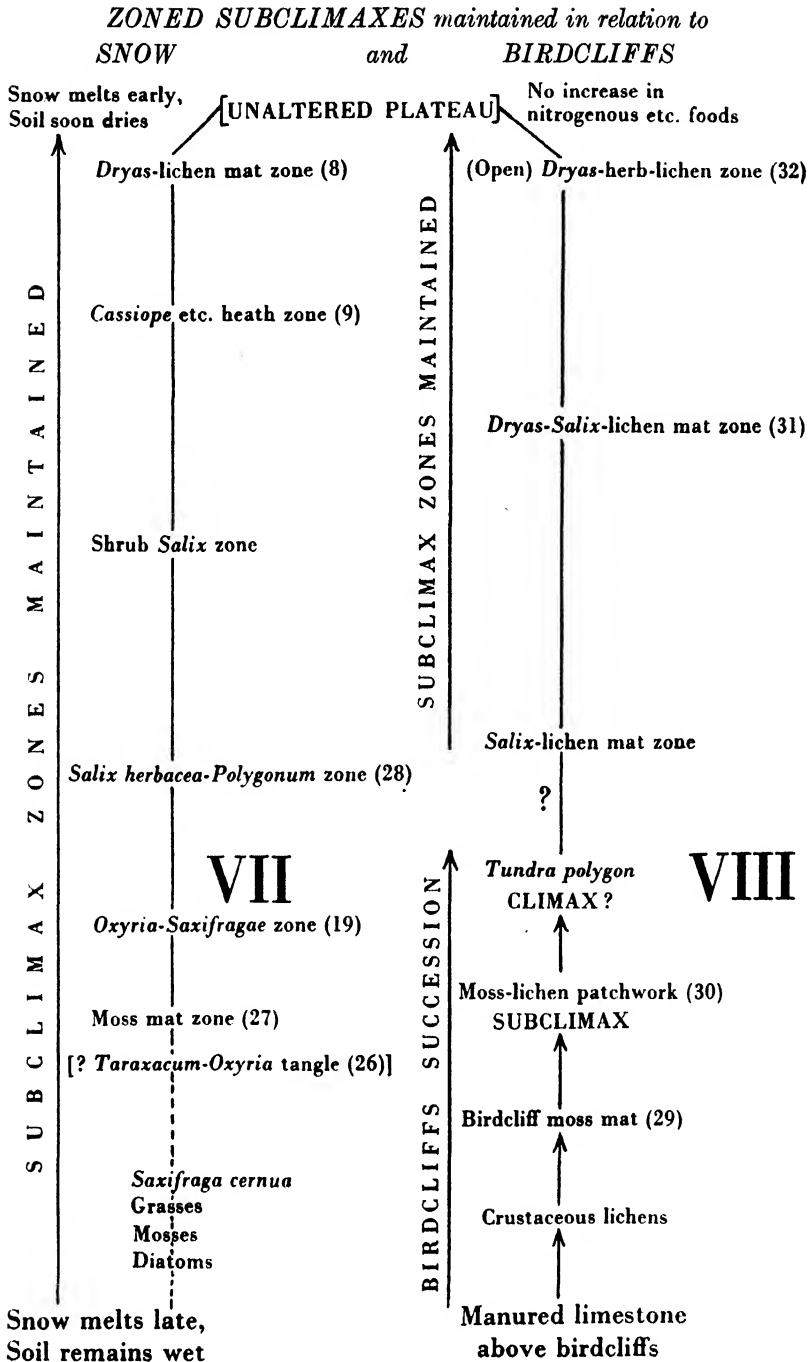


FIG. 3.

2. The semi-aquatics are more important, although again rather limited in species and in the conditions they can overcome. There is no *Sphagnum* on the island and its place is rather inefficiently taken by certain amphibious mosses of tufted growth. Indeed the semi-aquatic stage as a rule only occurs in fairly sheltered places, and then consists of BEDS OF *ERIOPHORA* (23), or sometimes of *Pleuropogon Sabinei* or sedges, which grow out into the water where the lake is shallow and muddy. Often they are the first colonists, but probably deposit humus quickly enough to raise the level of the lake margin, in time quite considerably, and so allow succession to proceed.

3. The later reedswamp stage is generally represented by a lush closed *ERIOPHORUM-CAREX* BOG (24) developing behind, and in exposed situations or pools (which presumably remain constant in height for a time in early summer, even if they later on lose water suddenly when an outlet is made by the melting of subterranean ice) it may be the first stage. In such cases the bog is often delimited by a definite line at the edge of the lake, as this appears in early summer, and extends, if at all, only very slowly at the edge by the growth of tussocky mosses or the rhizomes of the dominants.

4. Where the bed has become higher and drier by humus deposition under stagnant conditions it is usually colonised by *CAREX MEMBRANOPACTA*, which may be almost pure over considerable areas, although in wetter places cotton-grasses generally persist. Sometimes there may also be fine stands of *Arctagrostis latifolia*, with or without other grasses of such damp habitats having a deep humus soil. On the whole this drier bog supports a definite community (25), which is probably to be regarded as the sub-climax of the hydrosere. Approximations to it are maintained also in many damp depressions of the plateau which apparently never have any standing water.

5a. Behind, in ordinary exposed localities, this community passes (sometimes quite abruptly as the influence of the water is no longer felt and the region of the true hydrosere is left behind) into a plateau polygon area with its usual sparse open *DRYAS-SALIX-HERB* VEGETATION (6), although generally there are towards the edge a few hummocks of hillock tundra, sometimes covering more extensive tracts. Such areas are dominated by the usual drier lakeside community, generally by *Carex membranopacta*, but show in many cases an advance in succession, as willows colonise the tops of the drier hummocks.

5b. In sheltered valleys where the lakesides have a deep covering of snow in winter no hillocks are formed, but mosses clothe the ground between the shoots of the sedges and cottongrasses. More humus is laid down under the better conditions, and a fairly deep bog may result, whose mosses are able to extend into peaty pools or even moving streams of water. This mossy bog is colonised around its drier edge by willows and grasses (? Climax, see Fig. 2), and beyond, in sheltered regions, may support a heathy mat of ericaceous ground-shrubs which constitutes the post-climax of the hydrosere as of other seres.

VII. LATE SNOW ZONED SUB-CLIMAXES.

The *TARAXACUM-OXYRIA* TANGLE (26) of snow run-off holes is not properly understood, but may be a peculiar herb sub-climax belonging to the sandy soil series. In larger and later-melting snow patches, especially in valleys that are filled each winter with snow blown off the surrounding plateau, the following zones of vegetation are generally recognisable. They constitute a series of sub-climaxes, each zone being determined primarily by the time of melting, every summer, of the snow which covered its area during the winter, and secondarily to a certain extent by local water conditions. The zones also indicate the general successional tendencies, but here again comparatively little humus can be accumulated except towards the outside of the patch where the growing season is relatively long and the succession can proceed or be deflected; the autogenic effect of growing vegetation is largely overwhelmed by external factors. Starting from the centre of the patch as many as seven zones may be distinguishable:

1. In the centre of large patches whose snow only disappears at a very late date, or near the edge of ice which had not melted even at the end of August in 1931, there remains a zone which is generally quite barren, although there may be a shoot or two of *Saxifraga cernua* or small grass colonists, or a few little bright-green vegetative moss tussocks. Frequently there is merely a deposit of fine mud, whose surface may be brown with diatoms, or rendered still darker by layers of humus from decaying leaves and dust left each year by the melting snow, on whose surface such material is wont to accumulate.

2. Outside comes a typical MOSS MAT OF LATE MELTING SNOW (27), generally with a few saxifrages and sometimes grasses or leaves of *Cardamine pratensis*. There follow:

3. *OXYRIA-SAXIFRAGE* BARREN (19), comparable with that of wet valley sides, but generally drier and less extensive.

4. *SALIX HERBACEA-POLYGONUM VIVIPARUM* ZONE (28), a sub-climax which like the last may cover considerable tracts in large late snow areas on the sides of valleys. It is characterised by the accumulation of a thin surface layer of fine black humus throughout its area.

5. Shrub *Salix* zone, of *S. arctica* and *S. reticulata*, the latter appearing to be especially favoured by a good snow covering, at least on Akpatok.

6. A zone of *CASSIOPE, ETC.* HEATH (9) with *Dryas* and *Carex misandra*, comparable with other post-climax communities seen elsewhere, and again with a dark humous soil.

7. A zone of *DRYAS-LICHEN* MAT (8), with sedges and willows and sometimes other ground-shrubs. This is a mixed and variable community which represents apparently an approach to the post-climax of certain fjældmark areas, where there may be some shelter and a little snow covering at times, and an extra supply of water at the beginning of the growing season.

VIII. BIRD-CLIFF SUCCESSION AND ZONED SUB-CLIMAXES.

As in the case of late-melting snow there is maintained above the bird-cliffs a zoned series of sub-climaxes; but here the master factor is the increase in nitrogenous and other food materials afforded by the nesting birds and carried up mainly by scavengers. Zonation is seen along any line going away from the source of supply and as a rule regularly from the edge of the cliff. From these zones and from certain areas near the edge where the supply is less abundant or the nesting birds are only starting to colonise the edge of the cliff, the earlier successional stages may be inferred:

1. The pioneers are probably the crustaceous lichens and more conspicuous yellow and other foliose types which here, and here alone on the island, clothe the limestone boulders on the cliff-top with an almost continuous investment.

2. The more primitive lichens on smaller fragments of limestone lying on the ground seem to be followed quite soon by more highly organised types, which in turn are superseded by mosses that quickly form a thick mat very retentive of water. This luxuriant BIRD-CLIFF MOSS MAT (29) persists in damper depressions near the cliff edge, often uncolonised by lichens or vascular plants.

3. The mosses deposit humus, and as the tops grow up they become progressively drier and are colonised by lichens of luxuriant growth giving the characteristic "PATCHWORK QUILT" (30). There may also be numerous small grasses, and rosette and other herbs, such a community being maintained over considerable areas.

4. The climax under certain conditions seems to be of the giant "Tundra Polygons." These have a luxuriant moss community maintained in the intervening dips, with grasses, forbs and lichens on the mosses covering their dome-shaped tops, so that the area as a whole appears more grassy than the ordinary "patchwork quilt."

Other sub-climax zones which may extend to the edge of the cliff where the master factor is less intense, but which are generally more marked behind the patchwork quilt areas, are as follows:

5. Willows become more numerous on the quilt, and lichens more abundant than mosses, until a rather dry *Salix*-lichen mat may be developed in places.

6. With a still smaller growth of mosses to deposit humus and hold water, *Dryas* enters and the community passes behind to a very dry and thin *DRYAS-SALIX* MAT WITH MANY LICHENS (31).

7. Behind comes the change (sometimes abruptly, but more often gradually as the addition of nitrogenous food substances becomes less and less and finally almost negligible where the area is too far behind the cliff edge to be visited by scavengers) to (open) *DRYAS-HERB* FJAELDMARK WITH LICHENS OF POOR GROWTH (32); and finally we get the ordinary *DRYAS*, ETC. FJAELDMARK (5) of the unaffected plateau. There is no shelter on these areas behind the tall bird-cliffs, and since there is no proper snow covering in winter, no tendency to the

heath mat post-climax of ericaceous or other ground-shrubs was observed on them.

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SUCCESION, DEVELOPMENT, THE CLIMAX, AND THE COMPLEX ORGANISM: AN ANALYSIS OF CONCEPTS

PART II. DEVELOPMENT AND THE CLIMAX

By JOHN PHILLIPS.

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DEVELOPMENT: ESSENTIAL NATURE AND DIRECTION

HISTORICAL SUMMARY.

WHILE the process of *development* could have been logically discussed together with the process of *succession*, because of its intimate relation with succession, it serves my purpose of analysis better to deal with development separately. So closely interrelated, indeed, are the concepts of succession, development, the climax, and the complex organism, that it would be difficult, almost im-

possible, to investigate one concept without referring to this or that aspect of the related concepts.

Before summarising the more important features in the history of the concept of development, and without entering into any precise detail, it is desirable to explain broadly what this process is: that which is responsible for the origin, shaping, growth and reproduction of community structure—the grand resultant of the naturally related subprocesses of migration, establishment, growth, reproduction, competition, reaction and stabilisation.

According to Braun-Blanquet (1932, p. 305), Kerner (1863, p. 12) was responsible for the concept of the development of communities; Clements (1916, p. 22), however, records that the first to recognise fully the fundamental importance of the process in vegetation was Hult (1886, 1888), while the first to undertake a detailed study of the development of a great community was Graebner (1895, p. 58). Clements (1916, p. 28) rightly attributes great credit to Cowles (1899, pp. 95, 112; 1901, p. 73; 1909, p. 668; 1911, p. 172), referring to his work of 1901 as “a landmark in the developmental study of vegetation.” For certain vegetation in Nebraska, Pound and Clements (1898, p. 216; 1900, p. 365) gave developmental details; the earlier work of Clements (1902; 1904, p. 6; 1905, p. 199; 1907, p. 219) drew attention in increasing degree to the importance of development, both *in detail* and *in principle*. Moss (1907, p. 12; 1910, pp. 35, 36; 1913, p. 21) has been deservedly praised by Clements (1916, p. 118) and by Tansley (1916, p. 199) for being the pioneer in regard to considering development in the determination of plant *formations*. Moss’s emphasis upon the importance of the habitat, more especially the edaphic factors, unfortunately reduces—as Clements (1916, p. 124) too points out—the developmental value of his concept of the formation. Tansley (1911, p. 9) applied Moss’s concept of the formation, and other developmental ideas, to the classification of the vegetation of Britain.

As Cowles (1919, p. 417) has indicated in his review of Clements’s great book *Plant Succession*, Clements (1916, e.g. p. 136, etc.) laid stress upon *development* in the classification of vegetation, and defined a series of developmental units within the formation. Clements (e.g. 1920, p. 52; 1927, p. 327; 1928, p. 320; 1931, p. 266), and Weaver and Clements (1929, p. 90) have since added appreciably to the foundations laid down in 1916. From a study of many contributions upon the subject of succession, I agree with Braun-Blanquet (1932, p. 305) that “the principle of development is coming to replace the purely formal study of succession.” At the same time, I cannot help regretting that the replacement is not more general and more rapid.

VARIOUS THESES.

A perusal of the literature available leads me to arrange the ideas held and the problems raised by various workers under the following theses: (1) Development is due to biotic reactions *only*; (2) Development is due to

causes *including* biotic reactions; (3) Is succession developmental? (4) There is *no* development in plant communities; (5) Development is progressive only; (6) Development may be progressive or retrogressive.

I deal with these successively below, as briefly as possible:

Thesis: Development is due to biotic reactions only.

Development of the community from primitive, pioneer conditions to the ultimate or *climax* stage, is conceived as being due to reactions of living organisms—plants and animals, but more especially plants.

Organisms enter a habitat; the habitat acts upon them; they in turn react upon the habitat, altering it in terms of aerial and edaphic factors, and as to quantity and kind of the soil microflora and microfauna; the altered habitat in turn brings about a change in the composition and structure of the community.

It is essential to bear in mind that the *basic* causes of development reside in the habitat just as they do in the individual organism. But there is an important difference discernible when community and individual are contrasted precisely: in the community, biotic reactions produce a cumulative improvement in the habitat.

Inherent in the *full* acceptance of this view-point is agreement that the concept of development in the community has an analogy with development in the individual, development being of its very nature *progressive*, and the community being an integrated entity, a *quasi-* or a *complex organism*. Clements (1916, p. 3) puts this plainly: the developmental study of vegetation—he might have written *biotic community* to have made the reference all embracing—*necessarily* rests upon the assumption that the climax formation is an organic entity; to which assumption Cooper (1926, p. 399) takes marked exception.

That partial acceptance of this general concept has been found possible, is seen in the work of Moss (1913, p. 21), who speaks of the formation being, or having analogy with, an organism, who emphasises the importance of development in study of the formation (1907, 1909, 1913 *loc. cit.*), and who yet appears to believe succession—and I take it, development—to be either progressive or retrogressive.

It is, of course, to Clements (1905, p. 199; 1916, pp. 3, 4, 6, 125, 145; 1920, p. 52; 1921–33) that this concept is largely due, and it is based upon an abundance of observation and experiment on the part of himself and his collaborators during the past thirty years. A clear and simple expression of the concept has recently been made by Weaver and Clements (1929, pp. 3, 44, 55, 90). To Tansley (1920, pp. 132, 136–7, 146, 147; 1929, p. 678) we owe an excellent, balanced discussion, indicating clearly his view that it is only *organically controlled succession* in which it is possible to recognise development, that this kind of succession—development—is always progressive, and results in the mature *quasi-organism*, and that in development the plants are

the main controlling factors. He is convinced that to a succession mainly determined by the activities of the plants themselves and to none other, is it permissible to apply Clements's conception of the climax community as an organism.

It is distinctly interesting to notice the conclusions arrived at by Karzinkin (1927), who has attempted to establish by analysis of animals found on various hydrophytes and by a series of experimental changes of the habitat, the influence of general ecological conditions on *biocenoses*. Changes in the factors of the external biota or changes in the constituents of the *biocenose* disturb its equilibrium; but while such disturbance may be long-continued and complicated, equilibrium is ultimately again attained. It is possible, therefore, to speak of a *biocenosis* only when it reacts on the changes of the external and also of the internal factors, i.e. on its own constituent species; should such reaction be absent, the aggregation of organisms is simply an artificial, casual conjunction of organisms, and not a *biocenosis*. General agreement with the concept is shown by Shelford (1931, p. 465) who, however, desires to differentiate between succession and development; development should be understood to cover the growth of communities both where no succession occurs, and where succession is an outstanding fact.

In my own work (Phillips, 1931, pp. 203-9; 1931 *a*, p. 21) acceptance of the belief that development is due to biotic reactions only, and that succession is the development of the complex organism, the climax community, is implied. My reasons are given under "Conclusions" in the sequel (Part III).

Thesis: Development is due to causes including biotic reactions.

While it is admitted that biotic reactions play a part—perhaps a very important part even—in development, it is believed that other causes—such as aerial and edaphic factors—play a fundamentally influential rôle.

Cowles (1909, p. 668; 1911, pp. 171-2), while not subscribing to the view that development is due to biotic reactions only, is careful to stress the general importance and the comparative rapidity of biotic reactions in development of vegetation, concluding that if, in their operation, regional agencies are matters of aeons and topographic ones matters of centuries, biotic reactions may be expressed in terms of decades. With Tansley's (1920) suggestion, that a distinction should be drawn between *succession per se* and *development*, Nichols (1923, pp. 168-9) is satisfied, but takes a wider view of development than do Cowles, Clements, and Tansley: in his opinion, any succession is *developmental* so long as it is progressing to a climax. That he somehow senses the inherent connection between development and the complex-organism, the community, Nichols (1929, p. 638) shows by his conclusion: that the difference between the association, considered as an entity, and the association compared with an organism, is identical with the difference between succession and development pointed out by Tansley (1920).

Query: Is succession developmental?

Is *succession* wholly, partially, or in no way at all the process resulting from progression toward increased complexity, efficiency for a particular habitat setting, and maturity, that is, resulting from *development*?

We have seen that Clements (*op. cit.*) and others are definite that succession springs from development; conversely, Nichols (1923, pp. 168-9) conceives development proceeding apart from organic control, and Cooper (1926, p. 402) inquires whether the concept of development could, on justifiable grounds, be transferred to vegetation. Cooper fully appreciates that the "complex organism" concept of the climax community has had a good deal to do with this transfer; as he is opposed to this concept, he naturally finds it more helpful (p. 403) to consider succession simply as change, without associating with it the subjective concepts of progression, retrogression and *development*.

Thesis: There is no development in plant communities.

On this thesis it is held that so-called plant or biotic "communities" are mere assemblages of organisms, constituted largely by the chances of distribution and the suitability, or the reverse, of the habitat; the so-called "communities" possess no organic entity inherent in their history and structure; *development*, therefore, obviously cannot be considered apart from the development of each individual organism in the assemblage. While I admit I cannot trace in the literature any investigator who has expressed himself so definitely iconoclastic of ecological concepts as to voice entirely the view we are here discussing, I am tempted to refer to Gleason (1917, 1926, 1927, 1929) as one whose views on the *individualistic* concept of the plant community place him, in my opinion, in this general class. Gleason (1926, p. 23), after dealing with several examples which he considers illustrate his view, concludes that the vegetation of an area is merely the resultant of two factors—the fortuitous immigration of plants and an equally fluctuating habitat; hence there appears no reason for adhering to ideas regarding the definiteness and distinctness of plant communities. In the light of his remarks (1927, p. 308, etc.) upon rapid vegetational change following biotic reactions, I find it somewhat difficult to follow the logic of Gleason's various contentions.

Thesis: Development is progressive only.

Succession is the expression of development; development is an inherent process in the origin, birth, growth, structure, and maturity of the complex organism, the community; development in the individual organism is always progressive—*retrogressive* development is a contradiction in terms and in Nature—and development in the complex organism too is, and of necessity must be, *progressive*. In connection with our discussion of the thesis that succession is due to biotic reactions only and is always *progressive*, Clements (1916, pp. 145-67 etc.) is emphatic that development must of necessity be

progressive in the community as in the individual; to which Cooper (1926, p. 403) citing the example of "second childhood" in man, replies that there is precedent in the life of the individual organism for the admission of retrogressive changes in vegetation. Tansley (1920, p. 136), as we have already seen, differentiates between succession and development; development is always progressive, while succession may be either progressive or retrogressive. My own experience (Phillips, 1931, 1931 a, 1932, 1934) is in support of *development always being progressive*.

Thesis: Development may be progressive or retrogressive.

Development, being due to various causes, may, like *succession*, be either *progressive* or *retrogressive*; it is accepted that numerous examples of retrogressive succession may be found, and as succession and development are associated, development may well then be retrogressive.

As has been shown in our discussion of the concept that succession is due to any cause, and is either progressive or retrogressive, Cowles (1901, 1909, 1911, 1919, p. 477) is a supporter of retrogressive development; Moss (1910, p. 36; 1913, p. 21), from his treatment of retrogressive succession and retrogressive "associations," seems to have believed in retrogressive development, despite his wisdom in putting forward the fundamental utility of development in the classification of communities. In his treatment of habitat, Yapp (1922, p. 13) describes the "*successional habitat*," which undoubtedly is associated with *development* in the community; it seems that he accepted retrogressive as well as progressive development. Cooper (1926, p. 411), as has been shown repeatedly, is a keen exponent of the view that retrogressive development—if the concept of development really is justifiable at all—is a legitimate one. In dealing with development, Warming and Graebner (1933, pp. 400, 428; 1992) appear to accept retrogression. They illustrate (p. 400) retrogressive succession in the instance of the forming of raw humus in a beech forest, with consequent absence of beech regeneration, disappearance of the beech and conversion to *Calluna* heath; referring to Graebner's (1913, 1924) work, they describe (p. 1092) soil exhaustion under pine on the Lüneburger heath, with disappearance of this species about the third rotation. Cockayne (1911) is quoted by them (p. 428) as stating that the same climax is attainable from different initial stages, and may be the outcome not of progression, but of retrogression.

CONCLUSIONS.

I have already recorded that I am a supporter of the thesis that development is due to biotic reactions only, and of the cognate proposition that development is always progressive. It remains for me to add that the details, principles and philosophy of development may best be interpreted on the basis of the community as a complex organism. A summary of my reasons for these conclusions follows:

(1) Migration (including aggregation in the sense of Clements (1916, p. 63)), establishment, growth, reproduction, competition, co-action, reaction, maturity, and stabilisation are definitely under organic control and are inherent in the functions of the community itself.

(2) Integration within the community—the outcome of action, response, reaction—is under organic control; integration in behaviour is probably largely due to the fundamental process of development.

(3) In degree and in kind, biotic reactions are so active, so far-reaching in their results, that they cannot but be the central influence in development. While it is true that climate controls the climax, and thus sets an ultimate stage to the development of the community, this in no way detracts from the fact that biotic reactions are responsible for the details of development.

(4) Details bearing upon the sub-processes of competition, co-action and co-operation within the community are under organic control, play an important rôle in development, and are difficult of any kind of explanation if the community functions otherwise than as an organic entity.

(5) Retrogressive development in the individual organism is no less impossible than it is in the community; the analogy of senility in the individual is unsound, for senility cannot be interpreted as development.

THE CLIMAX.

HISTORICAL SUMMARY.

According to Clements (1916, pp. 22–3) Hult (1886–8) was the first to grasp the significance of the *climax* in vegetation. While we thus owe credit for the general concept to Hult, we do not find that he attempted carefully to analyse the concept, its many implications and ramifications throughout the whole field of the ecology of biotic communities. Pound and Clements (1898, p. 216; 1900, pp. 315–16) in their treatment of the origin and stabilisation of “formations” (communities), indicated that they were aware of the concept of climax. In his concept of *climatic* or district formations and *edaphic* or local formations, Schimper (1898) came very near the fundamental distinction between *developmental* and *climax* communities; undoubtedly many of his *climatic* formations are equivalent to climatic climaxes; his *edaphic* units being seral stages. As always we find Cowles (1901, pp. 80–1) keenly alive to fundamental principles in his conclusion that “societies” pass in a series of successive stages, from their original condition to the *climax* or culminating type. Highly important contributions to our knowledge of the process of stabilisation were made shortly afterwards by Clements (1904, p. 134; 1905, p. 324; 1907, p. 285), who definitely stated that *stabilisation* is a *universal tendency* of vegetation.

More recently Clements (1916, 1920; *vide* references 1917–34) and his associates have done much to investigate the process of stabilisation, and its end, the climax; all of this work has strengthened Clements’s (1916, p. 98)

earlier conclusion: the progressive invasion typical of succession everywhere produces stabilisation; the end of stabilisation is a climax; the climax is produced as the result of biotic reaction, within a definite setting, limited and regulated by the *climate*. Without entering into details (references are given under the section dealing with the *edaphic climax*), it is necessary to mention the work and views of Tansley (1904, p. 200; 1911, p. 9; 1913, p. 29; 1916, p. 199, 203; 1920, pp. 139–41) and Moss (1910, p. 36), supporting the thesis that there are not *climatic* climaxes *only*, but also *edaphic* ones.

VARIOUS CONCEPTS AND THESES.

Since the publication of Clements's views (1916) as to the control of the *climax* by *climate* there has developed an ever-growing storm of controversy regarding the nature of climaxes and the agencies responsible for their control. I discuss some of the conflicting views below:

Concept: The climatic climax: the climax is always controlled by the climate prevailing in the region concerned.

In its fullest expression this concept embraces the belief that the *climax* is the ultimate expression of *biotic reactions*—which are always *progressive* in their influence and direction—within the limits set by the *climatic* factor-complex of the region concerned. In other words, the climatic climax is the highest stage of successional development. That edaphic conditions, or external biotic agencies acting upon a community, are capable of regulating a climax, is not admitted; topographic, edaphic, biotic conditions may well impose a control upon succession, thus inhibiting or retarding the development of the climatic climax, but these conditions in themselves are, in the long run, overshadowed by the *master* control inherent in the climate. While the climate of any given region, in its prime factors and factor-complexes, lies within certain limits, it is realised that between these limits exists a veritable mosaic of *sub-climates* or *micro-climates*; and in response to such variations in the general climate there exist a number of *variations* in the climatic climax community.

The author and principal protagonist of this concept is Clements (1916, pp. 98, 106, 125–7; 1918, p. 373; 1920–1934 *vide* references), but much credit is due, as Gleason (1927, p. 316) points out, to Cowles (1901, pp. 80–1) as the pioneer in its introduction, in a less developed and less comprehensive form, into American ecology. As expressed in the definition given above, the concept finds *full* support from Clements and from myself (Phillips, 1926, pp. 365–7; 1927, pp. 333–4; 1930, p. 201; 1931, p. 363; 1931 *b*, p. 476). Cowles (1919, pp. 477–8) is a believer in the master control being wielded by climate, but as he urges (*vide* Cowles, 1919, p. 477) that succession and development may be *retrogressive* as well as *progressive*, and as he does not subscribe to the view that development is due to biotic reactions only, it would appear that he cannot be regarded as fully in agreement with the concept as accepted by

Clements and myself. There is little doubt that had Cowles's (1909, p. 669) suggestion, that in view of the increasing objection to the use of the terms "climatic" and "edaphic," there should be substituted for them the terms "ultimate" and "proximate" respectively, been carried out, much of the controversy regarding the relative rôles of climate and of edaphic conditions in limiting the climax, would never have arisen. It is interesting, however, to note that more recently Cowles (1928, pp. 381-2) in referring to the great treeless tracts of the Middle-west of North America—the prairie region—is strongly in favour of the views of Glinka (1914) and other Russian investigators, and of Marbut (1923), working in America and Africa, regarding phenomena of soil evolution as related to climate and vegetation. Cowles contends that prairie and forest, in the course of time, through biotic reactions and associated causes, would build up soils conspicuously different...provided they commenced upon soil of similar nature under similar climatic conditions; at the outset a very *minute* factor may have determined whether a prairie or a forest originated in a particular region, but as centuries elapsed, the determining factors became accentuated, the outcome being the firmer establishment of prairie on one site, the forest on the other. Thus down the centuries, prairie tends to persist on prairie soil, forest on forest soil, but a climatic change may favour now the encroachment of the prairie, now that of the forest. It may be pertinently suggested that Cowles, while conceding importance to biotic reactions, has failed to do so sufficiently, and further, has failed to take sufficiently into account that in regions where forest and grassland impinge or are mixed, protection of the grassland from grazing and fire accelerates biotic reactions on the part of the grassland tending to its own disappearance before the incoming forest stages; and that the potentiality for development from grassland to forest, in such instances, is inherent in the climate.

Braun-Blanquet and Pavillard (1922) believe that the development of plant communities is always toward the final climatic climax; Braun-Blanquet (1932, p. 255) more recently has stressed the relationship existing between vegetation regions, climatic regions, and soil regions, and especially the relation between the climatic climax and soils of mature, or climax, nature.

Since Braun-Blanquet (1932, pp. 310, 325) accepts the view that succession is due to *any* cause, and is either *progressive* or *retrogressive*—if progressive due to reactions, if retrogressive, due to causes other than reactions, it is clear that his acceptance of the climatic climax does not mean that he is fully in support of Clements's concept; this is the more clear when we read (1932, p. 315) that he looks upon the concept of the climax community being a complex organism as a flight of imagination. In insisting that the climax is not static, but "a breathing space in the ceaseless change of the composition of vegetation" Braun-Blanquet (1932, p. 322) uses the language of hyperbole, since some climaxes, at least, have existed for vast periods of time.

As presumptive evidence that *chaparral* is the climax in the broad-sclerophyll vegetation of California, Cooper (1922, p. 75) refers to dominance of the chaparral over a great range, its stability over a long period, its occurrence on diverse sites as to soil and topography, and finally its perfect adjustment to the climate. Later, Cooper (1926, p. 406) concludes that while *climate directs the larger currents of change*, the *details* are determined by biotic reaction, physiography, fire, and external biotic agencies. He does concede (pp. 408-9), however, that the additional complexities resulting from physiographic change, fire and man, are unable to deflect the main lines of progress governed by *climate* and evolution. Other views of Cooper are mentioned under appropriate sections in the sequel.

Rübel (1930, p. 32) accepts the climax community as the most complete expression of the vegetation of a definite climatic region; I suspect his views upon *succession* and *development* would tell against his being otherwise *fully* in support of the concept. Rübel's (1932, p. 4; 1933, p. 1059) later remarks about edaphic climaxes confirm this suspicion.

The opinion of Tansley is discussed under the section dealing with *edaphic climaxes*, but if I may refer to an unpublished communication from Dr F. E. Clements, it is of interest to record at this point that when Prof. Tansley writes of *the* climax, he appears always to mean the *climatic* climax.

To return to the views of Clements, it should be clearly grasped that it is argued that the *climate determines the dominant species* that are able to live within a given region, stage for stage, from the pioneer to the climax; the *order* in which these dominant species succeed each other is determined by the *biotic reactions*.

Concept: The edaphic climax: in addition to climatic climaxes there are edaphic climaxes.

According to this concept it is admitted that *climate* plays a fundamental rôle in limiting climaxes, but at the same time it is believed that *often*—the extent depending upon local physiographic and edaphic conditions—a *most important*, if not the *master* part, is played by *soil*. While the foregoing represents in essence the opinion of one school of investigators, it is desirable to state that certain other workers are inclined to attribute *much more importance* to the control wielded by *edaphic* conditions. I have met a few students of applied ecology—in forestry and grassland management—who indeed consider *climatic control* to play *little or no* part in the determination of the climax. Apart from the varying shades of opinion regarding the relative importance of climate and edaphic conditions, there are diverse views, too, as to the nature and direction of *succession* and *development*—tending to make impossible any satisfactory definition of the concept in terms of *control*, *dynamics of change*, and *direction*, unless recourse be made to somewhat considerable subdivision.

It seems that Hult (1886), the author of the concept of a *climax* in vegetation, believed that most communities are merely transitional stages towards a few final ones, the distribution of which is ultimately determined by *edaphic* conditions. As has already been pointed out, Schimper (1898) accepted *climatic* and *edaphic* formations; while he undoubtedly missed the distinction between *climax* and *seral* communities, he appears to have suspected that *edaphic* formations were transitional to the *climatic* ones. Although Warming (1909, p. 131) does stress the importance of soil in the distribution of communities, and appears to consider climate as of importance in the broad sense only, he also admits that climate may favour a certain community by causing this to be less exacting as regards *edaphic* needs, thus making possible its distribution over a large area on very diverse soils.

Among modern workers, Tansley (1904, p. 200; 1911, p. 9; 1913, p. 29; 1916, pp. 199, 203; 1920, pp. 139–41) has strongly advocated, on the basis of evidence gained principally within the British Isles and on the continent of Europe, the view that there are both *climatic* and *edaphic* climaxes.

Tansley (1911, pp. 9, 12) and his co-workers—principally Moss—in *Types of British Vegetation* defined the plant-formation as the plant-covering occupying a *certain type of soil*, characterised by definite plant communities and a definite flora; the formation is absolutely determined by habitat. Moss (1910, p. 36) had earlier more precisely defined the formation as the progressive “associations” (communities) which culminate in one or more stable or chief associations, and the retrogressive associations which result from the decay of the chief associations, so long as these changes occur on *the same habitat*. As Moss’s concept of the formation placed *habitat* in so basic a position, and as his concept was employed in the classification of communities described in *Types of British Vegetation*, it is readily understandable that soil conditions are given a most important rôle in this work. Tansley (1913, p. 29) in referring to some criticism on this point by Brockmann-Jerosch and Rübel (1912) in their attempt at a universal classification of plant communities, makes clear that such *edaphic* units were chosen because they represent actual natural units of vegetation to be found throughout the British Isles, an area possessing on the whole a relatively very uniform climate, and one in which the main differentiating factors are *edaphic*. In his able review of Clements’s *Plant Succession* (1916), Tansley (1916, p. 199) finds an opportunity of considering Clements’s concept of the *climatic climax* in relation to the deciduous forest of north-western Europe, the great semi-natural grassland communities of the British Isles, heath, and moor; he concludes that the restriction of the concept of the *formation*—the *seral* and *climax* stages of succession within a given climatic region, and not the climax stage, alone, as supposed by Tansley—to a *climax* stage determined by *climate* has practical drawbacks—it leaves out of account the establishment of *permanent* communities of distinct life-form, due to *edaphic* conditions or to conditions determined by *biotic reaction* on the

soil. In a discussion on concepts of the *formation* in vegetation, Tansley (1920, pp. 139–41) contends that the concept proposed by Moss (1907), developed by the same investigator (Moss, 1910), and embodied in *Types of British Vegetation* in 1911, undoubtedly enables a “perfectly good, workable, objective classification” of vegetation in England to be carried out—despite the criticisms that the *habitat* does not remain constant, but changes during development, that the naming of formations by habitats can have local significance only, and that the method is too subjective. Tansley and Chipp (1926, p. 8)—while agreeing that the *climatic climax* will *always* tend to develop on the *more favourable soils*—hold that there are good reasons for maintaining that certain kinds or conditions of soils render development of climatic climax *permanently impossible*—hence the ultimate vegetation upon such soils is best considered as an *edaphic climax*; such an *edaphic climax* may be a *climatic sub-climax*—the *soil type* holding the succession in a *subclimax* stage; or a special type of soil—for example salty soils and those of moors—may *divert* the succession, *ab initio*, into a different path. Essentially the same opinion is expressed by Godwin and Tansley (1929, p. 394), who consider that a soil factor may *deflect* the succession into an *edaphic climax*.

Dachnowski (1912, p. 31) writes of succession as a form of *edaphic* selection due to the establishment of certain species and the exclusion of others; elsewhere (1912 *a*, p. 259) he attempts to distinguish *climatic* and *edaphic* successions; as Clements (1916, p. 174) indicates, Dachnowski's *climatic* successions correspond to the *regional* successions of Cowles, his *edaphic* successions to the *topographic* and *biotic* successions of the same investigator; because the distinction is based upon initial causes it runs counter to the process of *development*.

Nichols (1917, pp. 313–14, 346, 348–9) has paid considerable attention to factors controlling the climax; I summarise some of the important features in his interesting paper. It is conceded that in the vast majority of areas there is a constant tendency for vegetation to approach the *regional climax association-type*—Nichols's (1923, p. 175) equivalent for the *climatic formation*; but *edaphic* factors not only influence the *rate* of succession toward the climax, but also determine the *extent* to which the succession can proceed; in *edaphically favourable* sites the *climax association-type* can be attained, in *edaphically unfavourable* ones the succession may be arrested at a point far short of this climax—such communities, although less mesophytic than the *regional climax association-type*, nevertheless are permanent with reference to the coeval climatic conditions, and must, therefore, be regarded as *climax*. Nichols is impressed with the relation of Liebig's (1843) “law of the minimum” and Blackman's (1905) conception of “limiting factors” with *edaphic* conditions, the degree of *mesophytism*, which he definitely correlates with degree of *ecological development*, being conditioned by the *limiting edaphic factor*. Tansley (1920, p. 142) points out that Nichols's conception of “limiting factors” and

the "*edaphic climax association*" corresponds with Clements's conception of *subclimax*—in the sense of "*proclimax*" as recently defined by Clements (1934, p. 45). While Nichols refers to Adams (1915) and Hooker (1917) in connection with these concepts of "law of the minimum" and "limiting factors," it is not out of place to draw attention to the thoughtful paper by Allen (1929) upon the "relative significance of variables," a concept, in my opinion, far more likely to express ecological relations than the concepts under discussion. In his suggestions regarding the application of the "law of the minimum" to problems in local physiographic ecology, Nichols (1917, p. 348) states that climatic factors, since they are essentially constant throughout the region, need not be considered—the variable factors are *edaphic*: due to variations in soil or topography. The fallacy of this generalisation is referred to later in this paper. In his reference to Tansley's (1916) objection to the restriction by Clements (1916) of the concept of *formation* to the *climatic climax*, Nichols (1917, p. 347) suggests the retention of Schimper's (1898) classification of *climatic* and *edaphic* formations, provided Schimper's views are modified to harmonise with the *developmental* concepts set out by himself.

It is instructive to note Tansley's (1920, pp. 142–3) treatment of Nichols's suggestions regarding the distinction of *climatic formations* and *edaphic* or *physiographic formations*: Nichols argues that the *climatic* habitat usually includes a number of *physiographic* habitats and thus a corresponding number of *physiographic formations*; Tansley aptly replies that the same types of *physiographic formations* frequently exist in more than one climatic region, examples being formations determined by extreme edaphic conditions, such as aquatic, subaquatic, salt-marsh and sand-dune vegetation. It is necessary, however, to mention that in a later work, Nichols (1923, pp. 172–3) emphasises that *physiographic climaxes* developed in any particular uniform climatic region, under favourable conditions of soil and topography, represent the *climatic climax*—that is, neither soil nor topography are able to exercise any limiting control; the *climax* vegetation is then the best expression of the influence of *climate* as a differentiating factor of the environment. Tansley, in dealing with Nichols's suggestion that the *whole* of the vegetation within a *climatic* region should be included in the *climatic formation* because it can develop under the climatic conditions provided, objects that as climatic regions cannot be sharply delimited, climatic formations in this sense cannot be distinguished: in the climatic formation it is permissible to include only *the climatic climax* associations and those communities which belong to them *developmentally*. As evidenced in a recent paper, Nichols (1929, p. 640), however, continues to differentiate climatic formations from physiographic ones.

Saxton (1924, p. 34) in discussing phases of vegetation under monsoon conditions, finds it difficult to avoid the conclusion that edaphic as well as climatic climax associations must be recognised. From this, he states, it

follows not only that there may be a succession of associates on any given site, ending in a *climax* association, but also that, by a change in the edaphic conditions, one climax association may gradually replace another on the same site...and the two climax associations may belong to *different formations*. He then contrasts his "mixed formation in time" (Saxton, 1922, 1924) with Clement's (1916) transitional communities in space: the *ecotone* and *mictium*. Finally, he advances the novel idea that two associations can, at least in part, occupy the same area at the same time!

The views of Du Rietz (1919, 1921, 1930, 1930 *a*) are mentioned in the sequel, in connection with the controversy of the "monoclimax" and the "polyclimax" concepts in vegetation, but it should be recorded here that he believes that several of his *climax-phytocoenoses* (Du Rietz, 1930, p. 338; 1930 *a*, p. 497)—often with very little relationship—may occur side by side in the same vegetation-region, but in *edaphically* different sites; by his use of brackets (p. 497) he appears to indicate that these edaphically conditioned climax-phytocoenoses are equivalent to the *edaphic* climaxes of Nichols, Tansley, and others. From the context and his citations, it seems as if Domin (1923), Gams (1918, 1923), Gleason (1917, 1926, 1927), Nordhagen (1927–8), and Scharfetter (1921)—in that they accept the *polyclimax* concept—are supporters of the existence of *edaphic climaxes*.

As is brought out in the discussion in the sequel, Gillman (1931–2, in manuscript; 1932, p. 4) a geomorphologist keenly interested in East African phytogeography, is a firm believer in the efficacy of edaphic and topographic features in determining vegetation communities and formations. Micheltore (1934, p. 315) from his remarks concerning the vegetation of a region not tending towards a single climax type, his remarks regarding soil influences, and the general context of his paper, appears to support the view that there are "climax types" determined by factors of *local climate* and *soil*, and possibly other features. From his investigation of the status of the pine community in Itasca County, North America, Grant (1934, p. 255) concludes that there is a conspicuous edaphic climax of Norway and White or Jack pine, and on peat soils an apparently stable *subclimax* swamp forest; as most of the surface of the country is either red drift or peat, the pine forest and the swamp forest cover many times greater an acreage than does the climax.

Bourne (1934), a forester, has vigorously criticised the *monoclimax* theory, and has emphasised the existence of edaphic climaxes with different dominants even within the same climatic region; he instances that in moist temperate regions peat soils with moorland climaxes alternate with degraded brown earths and forest climaxes, while in dry monsoon climates evergreen and deciduous forests are often associated, as distinct climaxes, with geological formations. Degree of extent of a climax provides no grounds for considering that climax as climatic, and other climaxes within the same region as edaphic subclimaxes: in the absence of disturbance they are all edaphic climaxes—

being relatively mature types with habitats in stable equilibrium. In his opinion, the real tests of a climax are stability of topography, maturity of soil in relation to climate, and presence of the climax dominants. In practice, he assumes until proved to the contrary that every topographic site or soil is potentially a climax habitat; for every potential *mature* site, a distinct vegetation *climax* is expected. Finally, he records his view that a climax is not necessarily identical with climate; indeed, the majority of climaxes are edaphic.

In the light of his work in Northern Rhodesia and his arriving independently at several of the conclusions recorded by Michelmores (1934), partly as the outcome of his studies in this part of tropical Africa, it is pertinent to refer to the fact that Mr C. G. Trapnell has informed me, in the course of correspondence, that difficulties in the way of the acceptance of a single climatic climax for the region which he has been studying are great, and that *tentatively* it is convenient to compromise between one *climatic climax* and a large number of unrelated *edaphic* ones. While Mr Trapnell has kindly furnished me with descriptions of his several edaphic types, and while Robbins's (1934) account of certain Northern Rhodesian vegetation types is helpful, I can pass no opinion upon the climax problem without having seen the region under discussion.

Concept: The biotic climax. In addition to being limited by climate and edaphic conditions, the climax may be determined by various biotic agencies.

It is believed by certain investigators that in addition to the control exercised by *climate*, *physiographic* and *edaphic* conditions, a *climax* control exists in the activities of *biotic* agencies. Among the more commonly cited, the more influential agencies are the various activities of *man*—his agricultural, pastoral, deforestation, reforestation, afforestation, and hunting pursuits being especially noteworthy—*grazing and browsing animals* under *feral* conditions, plant and animal *parasites* and *predators*.

It is necessary to state, however, that there are two distinct shades of opinion regarding the biotic climax and the principles of its development. On the one hand, there is the belief that all communities, therefore all climaxes, are constituted by interdependent plant and animal organisms with integrated responses, reactions, and co-actions: that they are neither plant communities nor animal communities, but *biotic communities*. In this sense the climax is *bio-ecological*, and to this integrated *plant-animal climax* Clements (1916 a) has given the term *biome*. On the other hand, there are those who believe that animals—and perhaps even parasitic plants such as bacteria and fungi—should be looked upon as *external* to the plant community: *biotic* agencies are accepted as being of fundamental importance in the life of the plant community, but as acting *externally*, and as able to impose from without some definite limitation as to the *climax* stage. This and associated points have been discussed by me elsewhere (Phillips, 1931 a), and receive additional attention under a special section in the sequel.

I attempt no more here than to refer to several investigators who are impressed with the importance of external biotic agencies in the determination of the climax—there is an ever-increasing tendency among workers in grass-land and pasture-management to utilise the concept *biotic climax* in the *second* sense mentioned above.

Bews (1920, p. 450), in discussing the plant ecology of the coast belt of Natal, and with special reference to the forest climax, expresses the view that animal agencies—notably insects attacking seeds—may prove more influential than the climate in bringing about changes in the climax.

I have recorded elsewhere (Phillips, 1931, p. 204) that from my own investigations in climax forest at Knysna, Cape Province, I found no evidence that biotic agencies could change the nature of the climax; at most they are responsible, in this region, for originating *subseral succession*.

Tansley (*vide* Cooper, 1926, p. 408; *teste* Clements, in correspondence) and Tansley and Adamson (1926, p. 32) are the best-known workers to use the term *biotic climax*; they use it to describe vegetation that has been kept in a state of equilibrium by grazing, for example by sheep and cattle, thus at a stage below the *climatic climax*; they state that in Clements's terminology their *biotically determined climax* is a *subclimax* (i.e. in Clements's (1934, p. 45) revised terminology a *proclimax*—J.P.). In a footnote to Godwin's (1929) treatment of the subject of "the subclimax and deflected succession," Tansley, in agreeing with Godwin that exception can be taken to the use of *subclimax*, in Clements's (1916, p. 107) *second* sense of a "kind of climax" or an "apparent climax"—because this means that the *subclimax* is not *really* a climax but only *seems* like one, whereas it *is* really a climax while the habitat, including the inhibiting factor, remains unchanged—explains that it is for this reason that the terms *edaphic climax* and *biotic climax* have been introduced for different kinds of climaxes resulting from permanent or semi-permanent action of an inhibiting, or often deflecting, agency. Godwin and Tansley (1929, p. 395) in their study of the *deflected successions* at Wicken Fen, say that a climax determined by the effect of grazing, or any other animal factor, is termed a *biotic climax*.

Where reference is made to natural grazing and browsing—for example by rabbits and deer in Europe—there could be no exception taken to the use of the term *biotic formation*, or *climax* in this sense, but where grazing and browsing pressure has been brought to bear upon vegetation by domesticated stock not normally associated with that particular vegetation, then application of the term does not appear desirable, or at least is not desirable so long as the term is used in the sense accepted by the believers in the concept of the *biotic community*. Shelford (1931, p. 464), in discussing "bio-ecological climaxes" of plants and animals, gives an excellent example, in my opinion, of a *biotic climax* in the sense of the *biome* or *biotic community* concept: if the bison held some of the mixed prairie of North America in a short grass stage,

then short grass is the *bio-ecological climax*, even if the *climax* without bison be quite different.

Chapman (1932, p. 328), a forester, in considering forest *types*, states that a *climax type* is assumed to be adapted to climatic and soil factors, with fire, imported diseases, insects, destructive winds, lumbering excluded, but that actually these may destroy the balance, and cause a change in *climax*. He is in favour of a *type* being conceived as that form of vegetation best adapted to survive not merely a few selected conditions like soil and climate, but *all* the conditions which will arise over the entire period of life of the individual trees of which it is composed. Biotic agencies in this particular instance, so far as I am able to understand, are looked upon as strongly influential *external* agencies. Davies (1933, pp. 8-9), a student of pasture management, believes that steppe, savanna and "natural" grasslands are true *biotic climaxes* developed under an extremely lenient form of grazing; they are *biotic communities* in harmony with a system of light grazing under *climatic* conditions that enable slow successional changes in the natural vegetation to take place; they are not functions of soil and climate alone. I desire to differentiate here between *natural* grazing and browsing due to animals *naturally* associated with steppe and savanna vegetation, and grazing and browsing by domesticated animals, that is, *man-governed*, often loosely known as *artificial* grazing and browsing. In the first instance, the climax resulting from animal relations is a *biotic climax* in the sense of the *biome*; in the second, animals bring about a *proclimax* in Clements's (1934, p. 45) sense.

Thesis: Succession does not lead inevitably to a definite climax, in fact succession never reaches a true climax. Query: Is there any climax phase at all?

While my knowledge of the literature available leads me to conclude that the only worker whose views tend to place him in the category of those who question the concept of the climax is Gleason (1917, 1926, 1927), I must record that among younger investigators and among students of applied ecology in agricultural, pastoral and forestry problems, I have encountered this conclusion more than once. As regards these classes of workers, the impression commonly existing, that the concept of the climax is too highly hypothetical, nebulous and subjective, springs naturally from two principal sources—one lack of experience and lack of knowledge of the literature, the other, failure to understand adequately the facts and principles upon which the concept has been developed. If I do Dr Gleason's views less than justice in my summary, I hope very much that he will forgive me and will publish the necessary corrections.

As long ago as 1917 Gleason advanced reasons for refusing to look upon the unit of vegetation as an organic entity, and strongly stressed the complete dependence of vegetation upon the phenomena of the individual. To these remarks Tansley (1920, p. 126) made clear and pertinent reply. In my treat-

ment of concepts of *development*, I have pointed out that Gleason's (1917, 1926, 1927, 1929) writings give me the feeling that he does not believe in *development*; a study of his expressed or implied opinions upon the *climax* lead me equally to feel that he is an iconoclast, too, in this particular respect. I refer to some of the opinions put forward in his 1927 paper. He asks (p. 312) whether succession inevitably leads to a definite climax, and replies that as "reversionary" successions certainly occur between different *types* and within a single *type*, succession obviously cannot lead to a *definite* climax. Next he enquires whether succession ever can reach a *true* climax; and on the grounds that the successional causes never cease to operate, that the so-called *climaxes* of the present will form the basis for further succession in the future, he replies that succession obviously never can reach a true climax. Later (p. 317) he states that the slow features of specific evolution and migration are sufficient, in themselves, to change completely the vegetation, whereas *climatic* changes may produce the same effect in even shorter time. He concludes (p. 317) that the climax "loses much of the artificial halo with which we have invested it," and that "in the long cycles of vegetative development [it] is merely a passing time-phase...."

Recently Tansley (1929, p. 684) has found occasion once again to refer to the tendency to throw doubt on the validity of the concept, and to defend the concept as being so firmly based on universally determined facts that its abandonment as the key-concept in the classification of vegetation, would, to his mind, be impossible. To his apt defence I desire to add, with Cooper (1926, p. 393), that the concept of the *climax* has become one of the keystones in the foundation of dynamic ecology. Details gained from studies in *distribution*, *succession*, *development*—all are against Gleason's conclusions.

Thesis: There is but one climax in any given climatic region—that is a climatic region in terms of vegetation response: the monoclimax concept.

Naturally any distinction between there being *one* climax, the *climatic*, or *more* than one, the *climatic*, the *physiographic*, the *edaphic*, the *biotic* and so on, is inherently interlinked with the consideration of the relative values of the *climatic* and other *climaxes*—hence it is unnecessary to do more than summarise the essential features in the two theories. For more detail, reference may be made to the foregoing sections.

Briefly, the "monoclimax" concept is held by workers such as Clements (*op. cit.*, especially 1916; 1920; 1932, pp. 214–15; 1934), Cowles (1901, 1909, 1911, 1919), Braun-Blanquet (1932, pp. 322–3), and Braun-Blanquet and Pavillard (1922; 1930, p. 15) who support the view that there is but *one true climax*, the *climatic*. My own experience (Phillips, 1926, 1927, 1930, 1931, 1931 b) is in full support of the concept. From his statement regarding the tendency toward *convergence* of all the unit successions of a region into a *single climax*—likened by him to the flowing of streamlets into a larger

stream—being a well-known phenomenon, Cooper (1926, p. 409) too is one of its protagonists.

As I have already said (Phillips, 1934, pp. 566–7), Clements (1926, p. 363; 1929, p. 198; 1930, pp. 236–7; 1932, p. 214) and Shelford (1932, p. 111) have provided for variations *within* the climax—in its final and its seral stages—on the basis of *local* climate and *local* edaphic variations. Further, Clements (1916; 1928; 1934, p. 45) and Weaver and Clements (1929) have not failed to take into careful account communities which are kept for any particular reason in an *actual sub-final* stage in the sere (i.e. a *subclimax* in the new restricted sense of Clements (1934, p. 45)), and those communities which are modified and held for a more or less indefinite period *in some other condition* (i.e. a *proclimax* in the new terminology proposed by Clements, *loc. cit.*). From the criticisms put forward by Bourne (1934, pp. 19–20), to the effect that Clements had conceived the “monoclimax theory” mainly as the outcome of his having worked largely in the prairies of North America, in a dry, continental climate, on a plateau of mature topography and soils—in fact the region furnishing the particular conditions under which the monoclimax theory is likely to apply in almost every respect, it is clear that this writer has missed two highly important points. Firstly, Clements’s experience during the past three to four decades has been infinitely wider than Bourne realises; secondly, Bourne seems to believe that within a so-called climatic region, the climate is uniform from boundary to boundary. In the very prairie region to which he makes reference as being so uniform, Clements (in correspondence, July 1934) has delimited *faciations* and *lociations*. The rainfall in this region varies from 35 in. in Illinois to 15 in. in Colorado. Throughout this great region there is but one great *climax* or *formation*, but it exhibits variations: between 35 and 25 in. the *climax* is the true prairie; between 25 and 15 in., the *climax* is mixed prairie. From Saskatchewan to Texas—in spite of marked temperature differences in human terms—both these associations extend throughout, but are marked by *faciations* with different groupings of dominants.

For a proper understanding of the bases and criteria of the “monoclimax theory” it is essential for the investigator to take into account such features as the following: (i) a climax is very rarely, if indeed ever, wholly uniform floristically and structurally; (ii) *relicts* are often present, such as persistent *seral* stages, *preclimaxes* and *postclimaxes*; (iii) *climax associations* making up the *climax formation* show *faciations* and *facies*, *lociations* and *locies* climatically determined, and *serations* edaphically determined; (iv) climatic cycles with reflections in the climaxes occur; (v) a climax is a “veritable mosaic”—to use Clements’s expression (in correspondence)—more especially since the development of agricultural, pastoral and forestry pursuits by man. Unless these be studied and interrelated, apparently contradictory and confusing impressions are certain to be gained, and to be published.

Thesis: There is more than one kind of climax: the polyclimax concept.

This has been mentioned sufficiently in the context to make further definition superfluous; the essential feature of the concept is that *climatic*, *physiographic*, *edaphic*, *biotic* and other kinds of *climax* are believed to exist.

The principal investigators responsible for the development of this concept have been Tansley (1911, 1916, 1920, 1929), Nichols (1917, 1923), Du Rietz (1919, 1921, 1930, 1930 *a*), and according to Du Rietz (1930 *a*, p. 346) the following Continental students: Gams (1918, 1923), Scharfetter (1921), Domin (1923), and Nordhagen (1927–8). Tansley has been the advocate of the climatic, the edaphic, and the biotic climaxes; Nichols has suggested the climatic and the physiographic (and edaphic).

Du Rietz (1930 *a*, pp. 497–9) cannot support the theory of the power of a uniform climate to transform *edaphically* different habitats into one comparatively uniform “climax-habitat” as required by the monoclimax theory. He believes that his *vegetation-regions* would coincide with the *climaxes* of Clements and the *Klimargebiete* of Braun-Blanquet (1930, p. 17; 1932, p. 323), but that each of these—in the instance of certain vegetation regions of Middle Europe and Scandinavia, and of New Zealand—would contain not *one* of his *climax-phytocoenoses* “of highest rank,” but *many*. Gleason (1917, 1926, 1927) is cited by Du Rietz (1930, p. 346; 1930 *a*, p. 497) as having aided in developing the polyclimax theory, but I prefer, in the light of Gleason’s (1927 *loc. cit.*) apparent doubts regarding the validity of the climax, to consider him as believing there is no climax at all.

In discussing some ecological concepts in their bearing on forestry, Bourne (1934, p. 16) has recently strongly supported the polyclimax concept, and has dubbed the monoclimax concept “of all hypotheses yet put forward, the most ambitious”; he affirms that evidence in support of the polyclimax concept is rapidly accumulating from all parts of the world. To his mind, the greatest hope of an early agreement between the respective adherents of the monoclimax and the polyclimax concepts lies in ranking Clements’s climatic climaxes with such vegetation regions as the Spruce-Fir Forests of the *Jura* and the Beech Forests of the Chilterns, and in the recognition that the vegetation of each such region, in the absence of disturbance, would yield a series of distinct climaxes. As he gives for the *Jura* the example of Spruce-Fir-*Vaccinium* climaxes in which the Spruce-*Vaccinium-Mulgedium* type is shown as a climax, and as he advances for the Chilterns Beech-Birch-Oak climaxes in which the Beech-Birch-Oak-*Leucobryum* type is termed a climax, I suggest that he consider the possibility of applying to these Clements’s concepts of *faciation*, *lociation*, and *seration*.

My stimulating critic, Michelmores (1934, p. 315), too, concludes that the vegetation of a region does not tend towards a single climax type; the real climax, or “natural” vegetation, is a whole series of types.

DISCUSSION OF CERTAIN CRITICISMS OF THE CONCEPT OF THE CLIMAX
AS APPLIED TO VEGETATION IN TANGANYIKA.

I desire here to discuss briefly certain criticisms by Michelmores (1934) and Gillman (1931, 1932) regarding my application of ecological concepts in Tanganyika Territory, and to summarise some points of importance regarding the relationship of fire and the climax.

CRITICISMS OF THE CONCEPT OF THE CLIMAX AS APPLIED BY PHILLIPS.

While some of the criticisms of my views to which reference is made in this section, and some of those to which I have drawn attention elsewhere (Phillips, 1934, pp. 564, 566-70), are directly concerned with succession and development, they naturally call for reply along with any criticisms bearing directly upon my concepts regarding the climax.

While I have already dealt briefly with some of Michelmores's (1934) objections (Phillips, 1934, *loc. cit.*), it remains for me to deal with several others. (1) Michelmores (1934, p. 313) is naturally averse to alteration in vegetation due to *physiographic* changes being described as true *succession*; I have already indicated clearly my view that *succession* is due to biotic reactions only, and thus is always progressive; my critic and I, therefore, have no difference of opinion on this matter. I am prepared to reconsider any of my suggested links of succession outlined in my work on the Central Province of Tanganyika Territory (Phillips, 1930)—if it can be shown that any of my suggestions refer, in reality, to changes due to *physiographic* causes as opposed to *biotic reactions*. It has been remarked by Gillman (1931), in referring to my record (Phillips, 1930, p. 214) of the gaining of my "Deciduous Scrub" climax upon my "*Berlinia-Brachystegia*" woodland, that in an area of interior drainage where a gradual spreading of aridity on to the higher slopes is what the geographer would naturally expect, such a change too would be expected. Apart from stating that such a gaining of Scrub upon *Berlinia-Brachystegia* is, in my opinion, capable of taking place where no drainage (due to the physiographic setting) is taking place, provided fire is excluded, I am naturally prepared to accept the possibility of the retardation, acceleration, deflection, interruption, or postponement of succession acting so as to complicate the normal sequences of development. Further work alone, and work of much more intensive nature than I was able to execute during my few years' stay in the region, will throw light upon these features, which are at present debatable. (2) Michelmores (*loc. cit.*) in referring to my linking up of communities in successional chains, indicates that I do not give my evidence. To begin with, I stated (pp. 193, 232) that the *suggestions* made were of a preliminary and tentative nature. Furthermore, my frequent references to reaction tendencies and structural and distributional phenomena should have made it plain that I utilised observations upon such features as relicts, zonation, alternes, tension zones or ecotones, ecoclines, regeneration, persistent seral stages, and growth-forms, to supple-

ment what a study of fire relations and protection areas were capable of suggesting. (3) Many of the *types* suggested by me are said by Michelmores (*loc. cit.*)—who admits he does not know the region—to be *soil types*, while others are suspected to be modifications due to fire and other causes. Apart from drawing attention to my subdivision of certain communities, of somewhat similar floristics and structure, on the basis of *eluvial* or *alluvial* soil differences, and to my specific treatment of *fire* influences not only in the work under discussion (pp. 231–2), but also elsewhere (Phillips, 1930 *a*; 1931), I content myself with pointing out that *soils* are under the developing, controlling influences of *climate* and *community*, and that there is no reason why soils of the most diverse types should fail to be able to carry vegetation types that will ultimately develop into the *climax faciation* or *location*, or another, for the particular *climatic* region concerned. In connection with Gillman's (1931–2) objection that plant communities, the distribution of which within a *climatically uniform* region depends on originally differing soils, cannot be brought into the same *successional* series, this matter is given further attention in this section. As Michelmores has cited Snowden (1933)—who worked in Uganda—as following me in linking up different soil types in one successional line, it would be interesting to have, sometime in the future, Snowden's reply, together with the observations of Greenway (1933, p. 33), and Scott (1934), workers in Tanganyika, who have followed my delimitation of climaxes.

Gillman (1931–2, 1932), who has criticised views put forward by me (Phillips, 1930, 1931 *b*), has dealt more especially with my suggestions regarding: (1) the relations of the *Berlinia-Brachystegia* woodland and the Deciduous Scrub climax; (2) the relations of the *Berlinia-Brachystegia* woodland, the peculiar *Grewia*-Other Species thicket, and the Deciduous Scrub.

(1) *The relations of the Berlinia-Brachystegia woodland ("Miombo") and the Deciduous Scrub climax ("Mchaka").*

Gillman's objection to my suggestion that "Miombo," provided disturbing factors like fire and fellings are prevented, is *developmental* on *eluvial* soils—the only soils on which it ever occurs—to "Mchaka" is based on the following argument. If *succession* implies the *development* of vegetation communities within a *climatically uniform* (italics his) region, and if *climax* means the final stage of the mutually dependent *development* of vegetation and soil under *unchanging climatic conditions* (italics his), then it is impossible to fit into one and the same *successional* series two such vegetation communities, typically representative of two very markedly differing climates.

The first point to which I wish to draw attention is his insistence on *succession* bringing about changes in a *climatically uniform* region. He himself goes on to explain, clearly and in detail, the relations existing among "tilt-block" structure, varied topography, and varied climate within a general region like the Great Central Plateau of Tanganyika, and, for East Africa in

general (*vide* Gillman, 1932-3), even goes so far as to correlate narrow, humid, well-watered *scarps* with forest, and much broader, much less humid *dip-slopes* with xerophile vegetation. Gillman is too good a geographer—indeed his power of tracing interrelations, from tectonic movements to plant and human populations, proves it—not to be aware of the importance of topographic features in making up a climate-mosaic influencing vegetation in the manner described by Shreve (1915), Vestal (1917, p. 355), Clements (1905, 1916, etc.) and many others. Robbins (1934, p. 93), in describing aerial photographs of vegetation communities in part of Northern Rhodesia, does a service by referring to his type VII on foothills, remnant rock and flat red soils, as showing several distinguishable forms that are constantly repeated, thus permitting their allocation to a type containing these as local variations: these variations are related to variations in slope, depth of soil and underlying rock. While Robbins's type is admitted to be an "artificial" one, and is comparatively limited in extent, it serves to illustrate the occurrence of *variants* within a general climatic region, which, if they occur in *climax* vegetation, form the larger *faciations* and *facies*, the smaller *lociations* and *locies*—*climatically* conditioned—and the *serations*, *edaphically* controlled. And yet, it seems, Gillman requires a *climatically uniform* region for *development*, I take it, of a *monotonously uniform climax*. Climatic control is basic, but never uniform from one end of a region to the other.

In the second place, Gillman appears to hold that *unchanging climatic conditions* are essential to *development* of the *climax*. I would invite his attention to the fascinating and fundamentally important matter of major and minor climatic cycles in "Recent" time, to the consideration of relationship between these changes and climaxes, and to the thought that climax alteration or shrinkage is a dynamic process under control of climatic change. In this connection, the accounts given by Clements (1922; 1925; 1931; 1933, p. 204; 1934, pp. 44, 49) are worthy of serious study.

Gillman continues that he knows of many instances where the *sudden* change, often without even the narrowest transition zone, from "Mchaka" to "Miombo" can be easily co-ordinated with the orographical features—generally and primarily influencing *exposure*—and this not only *regionally* but also with regard to the most intricate detail of the minor forms and changes of topography. I entirely agree that there is this constant alternation of the two communities, and I explain it in terms of differences in: (i) *successional rank*: due perhaps to age of the particular community, efficiency of the *biotic reactions*, and history of disturbance, e.g. by fire; (ii) *soil types*: "Miombo" is never found upon *alluvial* soils, whereas "Mchaka" may be found upon *eluvial* and *alluvial*: given time and protection "Miombo" on eluvium will develop to "Mchaka"; (iii) *nature of ecocline*: whether the aspect is cooler and more humid (*mesocline*), or warmer and more arid (*xerocline*): different *microclimates* are associated with difference in *ecocline*.

That the two communities actually exist within the same general mosaic of micro-habitats within a general climatic region in the portion of Tanganyika with which I am dealing, is, I suggest, a strong argument in favour of their being related *successionally*. It is worth while recording that the two communities and transitions between them are mentioned, for the same general climatic region as that dealt with by me, by Nash (1930, p. 326), Jackson (1930, p. 498), Greenway (1933, p. 33), and Scott (1934). It is strongly in support of my suggestion that "Miombo" is *seral* to "Mchaka," that Scott (1934, pp. 221, 227) should be able to report, even after two years' protection of "Miombo" from fire, a *well-marked decrease* in the numbers of seedlings, suckers and coppice of *Berlinia*, and a *definite increase* in "Mchaka" elements such as *Commiphora*, *Dalbergia*, *Dichrostachys*, *Harrisonia* etc. Trapnell (1934), in commenting upon *Isoberlinia-Brachystegia* in Northern Rhodesia, says (*in litt.*) that, so far as he knows, nothing in that country corresponds with my type (5) (Phillips, 1930, p. 214), but that many of the associated species mentioned by me would certainly be regarded by him as a possible sign of succession toward Scrub, if found in Northern Rhodesia; the grass layers as described are also suggestive of a "Scrub site." Mr R. R. Staples of the Veterinary Department, Tanganyika, informs me in recent correspondence (1934) that he is inclined to favour Gillman's view that "Miombo" is a *climax*. The essential edaphic difference separating it from Deciduous Scrub, he suggests, is possibly that the soil moisture is somewhat higher in "Miombo." If this be so, he argues that if fire be eliminated and if woody species increase to such an extent that soil moisture is reduced, Deciduous Scrub species will tend to invade, and under conditions of higher rainfall, Evergreen Forest species also. He prefers to consider "Miombo" as a different *formation* from Deciduous Scrub—the *Dry Forest formation*. As development from "Miombo" to Deciduous Scrub appeared to me to be accompanied by an increase in organic matter and in water-retaining capacity of soil, I cannot, in the absence of definite quantitative data, agree with Staples that the moisture values in "Miombo" are always higher than they are in Scrub. At all events, invasion of "Miombo" by Scrub species is not usually explicable, on grounds other than *succession*—the influence of physiographic features inducing drainage or increase in water content in certain kinds of sites naturally being accepted as working *with* or *against* the *successional* tendency.

(2) *The relations of the Berlinia-Brachystegia woodland ("Miombo"), the Grewia-Other Species ("Itigi") thicket, and the Deciduous Scrub ("Mchaka").*

I have described (Phillips, 1930, pp. 217–19; 1931 *b*, p. 372) for the southern and central portions of the Kilimatinde-Turu High-Block—as Gillman calls the particular region in Tanganyika—a peculiar type of vegetation: my *Grewia-Pseudoprosopis-Bussea-Other Species* Deciduous Scrub, called by Swyn-

nerton in various reports on Tsetse-fly, the "Itigi thicket"—Itigi being a station near a vast area of this vegetation. Geologically, this block—which lies approximately between 1000 and 1400 metres elevation—consists of granite, which is covered for hundreds of square miles by a peculiar *grey cement*, which Teale (1931, p. 13; 1933, p. 15) describes as reminiscent of Woolnough's "*duricrust*," ranging from a few inches to a hundred feet or more in depth, and very likely the result of Pleistocene peneplain conditions of drainage. Teale (1931, pp. 13–14) states that this cement is typical of the character of an *eluvial* granitic material subjected to subsequent transport; as it apparently represents an aggradation phase of the final peneplanation stage, whereby the *eluvial* decay of adjoining granitic and gneissose relics has been transported to neighbouring depressions, it seems preferable to consider the deposit as *colluvial* rather than *eluvial*.

On the gently undulating peneplain itself, the cement is broken ever and again by hills and ridges, remnants of a former erosive cycle, and composed of granite; on the stepped scarps in the east, the scarp slopes are of granite, while the surfaces of the steps still show remnants of the cement. Owing to back-cutting and other forms of erosion, the cement has been, and is being, removed from the granite, in a complex mosaic. Gillman (1931) and Teale (1931, *loc. cit.*), who have been responsible for the description of the geology and geomorphology of the region, point out that the sudden change from cement to granite is invariably correlated with a change from "Itigi thicket" to "Miombo." I must admit I was unaware of this particular feature until it was explained to me by Gillman; after I left Tanganyika my defence, if any be needed, must be Teale's (1931, pp. 13–14) somewhat comforting statement that it has been mistaken by prospectors and even by some geologists for decomposed *granite*—and by one noted German geologist for a trachyte! The granite soils are said to be more sandy, the cement soils to be richer in clay, a feature not unlikely to have a bearing upon their relative water-retaining-capacities. In this connection, it must be mentioned that Gillman records that, as a rule, the slopes of the *cement* peneplain are very gentle, while *granite* generally out-crops on the steeper slopes, a condition which undoubtedly must influence ground-water relations.

Climatically, as I have described elsewhere, the region covered by "Itigi thicket" on cement and by "Miombo" on granite is remarkably uniform, but Gillman points out some interesting features. Between 950 and 1350 metres elevation, both the scarp face and the level plateau very gently inclined westward, have practically the same exposure and therefore the same humidity. The lowest 100 m. or so of the scarp, however, which lie below, i.e., outside, the beneficent influence of the belt of increased condensation, participate in the markedly more arid climate of the Bubu river depression, and therefore carry neither "Miombo" nor "Itigi thicket," the place of both being taken by the normal deciduous thorny scrub characteristic of this climatic type. The

result is that, below 950 m., *granite* and *cement* are no longer separators of plant communities.

I have pointed out (Phillips, 1930, p. 218) that the successional relations of the "Itigi thicket" are obscure, that the appearance of occasional *Commiphora* spp.—typical elements of Deciduous Scrub—suggests little as regards *development*; but that the appearance here and there of what seem to be relict—they are usually old and not vigorous—communities of *Berlinia-Brachystegia* suggests that the thicket has succeeded the *Berlinia-Brachystegia*-Other Species Woodland, which has been unable to re-establish itself under the dense conditions of stocking prevailing in the thicket. Gillman, however, states that these communities of "Miombo" are, in the light of their relations with outcrops of *granite*, clearly proved to be *edaphically* determined, and thus far from indicating a succession from "Miombo" towards a thicket *climax*. On the contrary, he contends, there is definite proof of a gradual but continuous displacement of thicket by "Miombo"—not due to *succession* at all, but the result of a very distinct change of soil conditions due to purely tectonic causes and their morphological consequences. Accordingly, he sums up that "Miombo" and "Itigi thicket" are communities, the distribution of which, over a *climatically* uniform region, depends on that of originally differing soils; thus they cannot be brought into the same *successional* series.

To my mind, Gillman, although he has thrown light upon the *edaphic* relations of thicket and "Miombo," has by no means given the correct interpretation of the "Itigi problem," nor is he justified in the generalisation that communities distributed, in a *climatically* uniform region, in accordance with distinct *soil* types, cannot be in the same *sere*. As regards the action of physiographic factors, as described by Gillman, it is of interest to note that Fuller (1923, p. 140), in his account of an *edaphic* limit to forests in the prairie region of Illinois, concludes that yellow-grey silt loam regulates the presence of forest, which is nowhere present on brown silt loam; as the yellow-grey silt loam is uncovered by erosion, its extent is being gradually increased, and this extension is resulting in the gradual advance of forest upon grassland. Petrie, Jarrett and Patton (1929, pp. 244–6), working in Australia, have given details regarding a so-called "reversible *sere*"—which they state is in *no sense developmental*. The process of erosion, forming ever deepening valleys in the hills, apparently results in what I should term *succession-acceleration* towards a climax *Acacia-Nothofagus* community—this in response partly to increased shelter, humidity, and shade; when denudation of the hills proceeds so far as to convert the valleys into wide and shallow ones, shelter, humidity, and shade decrease, the *Acacia-Nothofagus* association yielding place to *Eucalyptus* communities and finally to the earlier *Pomaderris* and *Cassinia* communities: an example of what I should consider as a combination of *succession-retardation* and *-postponement*.

That the interaction of climate, physiographic agencies, activities of man and the response in vegetation is undoubtedly highly complex and requires

careful study before speculations are made regarding *succession*, is well exemplified by Bryan (1928, p. 477), who, in describing the change in plant communities with change in ground-water level near Tucson, points out that the deepening of the stream beds is associated with over-grazing by domestic stock—the consequent loss of vegetative cover in turn increasing the erosive power of the streams. He believes, however, that the fundamental cause of *arroyo* or channel cutting may have been a change to a drier climate, the over-grazing acting as an accessory factor which conditioned the date at which this cutting might commence.

So far as the "Itigi thicket" problem is concerned, it is difficult to clear up the matter definitely, because of our still too meagre knowledge both of the dynamics of change in the communities, and of the soil and soil water characteristics. I suggest, however, the following explanation. *Cement on the plateau*: soil finer, perhaps water-retaining capacity and water-supplying power higher; thicket may be a *postclimax* on account of the better soil water values under the less arid climate of the plateau—the absence of thicket on *cement* at lower, drier levels is suggestive in this connection. *Granite on the plateau*: Soil coarser, perhaps water-retaining capacity and water-supplying power lower; removal of *cement* from *granite* brings about less favourable ground water conditions—hence removal of conditions holding the *postclimax* thicket in position; this enables the Miombo to enter, and through the Miombo nurse stage, the *development* to Deciduous Scrub, elements of which have been described by me as being present from time to time. *Cement and granite at lower levels*: Deciduous Scrub covers these; the possibility of there being *lociations* and *serations* correlative with soil type is worth investigating.

As regards Gillman's criticism that plant communities distributed within a climatically uniform region, in accordance with the distribution of originally differing soils, cannot be in the same successional series, I invite attention to my remarks published elsewhere (Phillips, 1928, 1931, 1934, p. 658) referring to different *types* of the *climax* or other communities existing upon different geological formations and different soils, yet all definitely related successional-ly. In any case, *types* (*serations*, *locies* and *lociations*, *facies* and *faciations*) of Miombo, *Combretum*-Other Species Open Woodland, and Deciduous Scrub existing upon soils of different types, under similar or identical climatic conditions, must be well known to Gillman from his East African experience. Clements (1934, in correspondence) gives several American examples bearing upon my argument: (i) Douglas Fir near the Alpine laboratory, Colorado, is found as a *consociation* upon coarse gravel, but on the Pacific coast grows best in a fine, mature soil; (ii) the "Pine Barrens" of the East, almost universally assumed to be a response to a sandy soil, is clearly a fire *subclimax* to deciduous forest, which thrives equally well in such soil when fire is eliminated; (iii) the "Cross-Timbers" of Texas—see Clements (1934, p. 44)—are *postclimax* relicts of the deciduous forest climax, persisting because of the compensation afforded

by the available water-content of sandy soil; (iv) the sandhills of Nebraska are characterised by *postclimax* tall grasses, due to the compensation for lower rainfall afforded by the available water-content of sand; the tall grasses, however, everywhere yield to the mixed prairie as *reaction* renders the soil finer and the available water-content lower. Numerous examples of a similar kind could be given for South African grass savanna, tree-and-grass savanna, scrub and forest.

To my mind these and many other similar examples strongly argue in favour of the *master control by climate* over-riding such local differences as physiography, geological formation, and soil type.

FIRE: ITS INFLUENCE UPON THE CLIMAX.

I have indicated elsewhere (Phillips, 1926, 1930, p. 355; 1931, pp. 233-7; 1931 *b*, p. 372) the fundamental rôle played by fire in successional relations in South and East Africa. Gillman (1931-2, in manuscript) chides me for making fire the "supreme Leitmotiv" for the development of climax vegetations in Tanganyika, quoting in support of his comment my statement (1931 *b*, p. 372) regarding the vegetation of the Great Central Plateau Region: "Study of the vegetation of this great region shows that fire has played an important part in the development of the communities; apparently the ultimate expression is the Deciduous Scrub, but the stages leading thereto are inhibited in development by fire." My attributing "an important part" to fire in no sense implies that I make fire the "supreme Leitmotiv."

Indeed, Gillman's reference a little later in the same manuscript criticism (1931-2) to the question of the activities of man helping or hindering the problematic tendency of East African climate to become more humid or more arid, includes the remark that among man's activities, "his fires probably occupy the front rank"!

As is shown by Clements (1934), the influence of fire upon *succession* and the *climax* is really difficult to over-emphasise. What is really required are more detailed studies of the interrelations of fire, habitat changes, and phenomena of *development*—the good pioneer work of Clements (1910), Show and Kotok (1924), Larsen (1929) and others, has to be carried a good deal further. For brevity and clarity, I discuss the principal interrelations of fire and the *climax* under four heads:

(1) *Control of stage of succession by fire (succession-retardation).*

Chipp (1926, p. 228), on the grounds that fire in most instances is caused by man, terms fire a *biotic factor*; Clements's (1916, pp. 58-9) inclusion of fire among *biotic causes*—as opposed to *biotic reactions*—while distinctly preferable, does not take account of the fact that fire in certain instances is caused by lightning, fall of igneous rocks, and thermophytic bacteria (*vide* Clements, 1916, p. 157; Phillips, 1930 *b*, p. 352 *re* lightning and cause of fire).

In Africa, Busse (1908), Jaeger (1911), Obst (1923), Bews (1927, p. 111), Henkel (1928, p. 41), Galpin (1926), and Phillips (1926, 1930, 1930 *b*, 1931, 1931 *b*), among others, have been impressed with the influence of fire in retarding development toward a climax. The keeping out of fires, for example, by conscious protection, or by unintentional means, such as heavy grazing by stock, resulting in so poor a grass cover that fires are impossible, has certainly resulted in the development of woody scrub of various kinds, in South Africa and in East Africa; in South Africa classic examples of scrub development, scrub rich in numbers of *Acacia*, are seen in such areas as the Springbok Flats of the Transvaal, and in the Cis-Kei of the Cape Province, the midlands of Natal and the northern to north-western portions of the Orange Free State. Observations such as those by Hensel (1923, p. 183) in the Santa Rita Range, Arizona, supporting the view that Mesquite (*Prosopis*)—also a legume, like *Acacia*—has formed extensive shrubberies as the outcome of long-continued protection of grassland against fire—regular burning at the right season being suggested as a means of its control—have recently been contradicted by the work of Clements (1934, pp. 61-2) mentioned under head (2) below.

Tansley and Chipp (1926, p. 147), in connection with the destruction of forest growth, primary and secondary, say that this often leads to the occupation of the ground by a “new climax,” the *fire climax*, i.e. a *proclimax* in the sense of Clements. An interesting example of control by fire is mentioned by Cooper (1926, p. 108) in his review of the work by Show and Kotok (1924), who suggest that the immensely predominant Douglas Fir in the Puget Sound Forest is not the true climax, but owes its control to fire; again, in California, the Yellow and Sugar Pines may not be climax, but owe their predominance to fire. From India, Troup (1926, pp. 304, 306-8) gives *Shorea robusta* (“Sal”) and Bamboos as forming “fire-climaxes.” The intricacy of the *successional* stages in forest, following fire, has been discussed by Larsen (1929, p. 68) and Phillips (1931, pp. 233-37) for Idaho, North America, and Knysna, South Africa, respectively. For Australia, we have the record of Petrie, Jarrett and Patton (1929), who regard the forest fire as a great simplifying factor in the *development* of communities, which has led to the elimination of types not possessing powers of rapid regeneration; fires, too, considerably modify the community structure, resulting in increased density and purity, as well as in greater equality of age among their components. For the “monsoon” type of deciduous woodland termed by me (Phillips, 1930) the “*Berlinia-Brachystegia*-Other Species Woodland,” the observations of Wigg (1928), Phillips (1930), and Scott (1934, p. 228) support some of these statements by the Australians. While Wigg would consider this community as “probably the last term of a fire climax series,” I have described it as a *subclimax* (now a *proclimax* in the new terminology of Clements) due to fire, a view to which Scott has subscribed.

(2) *Quickening of succession by fire (succession-acceleration).*

From time to time it is found that fire, because it destroys some very slowly changing stage, or some *proclimax* community, results in a marked stimulation of succession (*succession-acceleration*) through the removal of the hampering community, the making possible of invasion and *development* of more active communities and the amelioration of edaphic and aerial conditions of the habitat. Ewing (1924, p. 266), for the Brush-prairie of north-west Minnesota, records that burning has been a frequent event in the history of the region, and has reduced the abundant water content of the various habitats; thus, where water insufficiency is not a limiting factor, the habitats have become more mesophytic. Without giving details to elucidate his statement, Stamp (1926, p. 247), in referring to deciduous Monsoon forest in Burma, says that these forests—through the destruction of undergrowth, and, I take it, the development of gourmand sprouts—*benefit* from fire, whereas the evergreen forests, of course, suffer badly.

In my own experience (Phillips, 1926 *a*; 1931, pp. 236–7), I have met several examples of *succession-acceleration* due to fire, of which I mention one only. In the Knysna forests, fire, in certain sites, results in the development of extensive areas of a community termed by me the *Gleichenia polypodioides* consocieties. *Gleichenia* is a rampant, prostrate and “climbing” fern, which builds communities up to a height of 5 to 15 feet, and forms in the course of time impenetrable masses of raw or decomposed stem and frond debris, highly retentive of water, and not allowing the establishment of most other species of plants. Unless vigorously disturbed, the fern appears to remain *in situ* for many decades, effectively keeping back succession toward climax forest. Should the community be removed by man, or should it be very severely burned during dry spells, other plants are able to establish themselves and to keep the fern from becoming dominant again, thus leading towards a higher stage of development. This is especially true if seeds of the arborescent *Virgilia capensis* and the shrubby *Psoralea pinnata* be present: fire accelerates their germination, the rate of growth of seedlings and saplings is very high, and within a comparatively short time a dense community of one or other, or both, these plants effectively keeps out *Gleichenia* and provides helpful conditions for seedlings of higher stages. Clements (1934, pp. 61–2), in discussing the Mesquite of Arizona—which he looks upon as *postclimax*—emphasises that the current assumption (e.g. Hensel, 1923, p. 183, already mentioned) that fire favours grassland at the expense of Mesquite is incorrect; all the evidence demonstrates that instead of this plant being reduced by prairie fires, it has been decisively favoured by them as the outcome of more efficient sprouting due to fire stimulus. In South Africa, a similar kind of behaviour is shown by *exotic* species of *Acacia*: firing results in their rapid and enormously effective multiplication from seeds and root-suckers. Various examples from the native flora, too, could be given,

notable among which are several species of *Acacia*, *Dichrostachys*, and other legumes.

(3) *Influence of fire upon important animal associates in the climax.*

Whether we accept the concept of the biotic community or whether we are content to consider animals as external biotic factors acting upon the plant community, we must realise the far-reaching results brought about, among certain classes of animals, by fire. Without doing more than cite the summaries given by Rice (1932, p. 400) and myself (Phillips, 1930 *b*, p. 339), I wish to emphasise the necessity of much more detailed work on this really fundamental point.

(4) *Fire and certain growth-forms in vegetation communities leading to the climax.*

The possibility of growth-forms of the woody plants of tree-and-grass savanna being influenced in their development by ever-recurring fires has been touched upon briefly by Gibbs (1906), Busse (1908, p. 127), Bews (1925, p. 180, 1927, p. 74), Henkel (1928, p. 51), and myself (Phillips, 1930 *b*, p. 358). All these authors are inclined to suspect some positive correlation. If such a correlation were proved to exist, the interrelations of fire and seral stages—in terms of specific abundance, relatively specific branching habits, and the like—would be even clearer than at present. Thus, it is interesting to note that Petrie, Jarrett and Patton (1929, p. 277), in referring to so-called “adaptations” to fire in regeneration stages, conclude that all such “adaptations” were existent before ever fires became a factor, and that such “adaptations” are in no way special responses for pyric regeneration.

SUMMARY OF MORE IMPORTANT CONCLUSIONS REGARDING THE CLIMAX.

I summarise those conclusions regarding the *climax* that I consider the most important, in the hope that they will call forth criticism, constructive or destructive.

(1) The contention that biotic communities—or, for that matter, *plant* communities—show no tendency to develop to an ultimate condition of dynamic equilibrium—the *climax*—is altogether against the facts, and cannot be considered seriously.

(2) The monoclimax theory is based on natural facts, is logical, and is capable of explaining—in the present state of our knowledge at all events—more satisfactorily than the polyclimax theory the various phenomena associated with *succession*, *development*, and the *climax*.

(3) The only true climax is the climatic climax: edaphic, biotic, fire, and all other so-called climaxes are capable of partial or complete explanation on the basis of the climatic climax. Unless the term “biotic climax” be used in the sense of the climax of an integrated biotic community, I suggest that it be

dropped, as its use in two senses cannot fail to confuse. As concerns the term "climatic climax", I have noted for some time that the use of the adjective "climatic" appears to mislead those not familiar with concepts and literature to think that there are other kinds of climaxes, e.g. an edaphic climax. I suggest, therefore, that the word "climatic" be eliminated; we should rather speak of *the* climax.

(4) Despite his criticism that the word "climax" and other terms descriptive of it—*vide* Hansen, 1921; Warming, 1896; Lüdi, 1919; Furrer, 1922—are unfortunate in their connotation of *finality*, Cooper (1926, p. 407) wisely concluded that to uproot it would be an undesirable, indeed a hopeless task. I cordially agree: in this instance, as in so many others, etymology must yield again to usage, and to special usage. By "special usage" I mean that to the ecologist the term must convey more than its ordinary meaning to the layman; this point is dealt with more fully under (5).

(5) The *climax* should not be conceived as being in *permanent, static* equilibrium with the climax habitat; it is more naturally conceived as being in *dynamic* equilibrium—adjusting here, adjusting there, showing this, that and the other internal alteration to accommodate itself the better to the ever-continuing alteration occurring in the habitat: alterations that the community itself to a great degree, and climatic swing to a varying extent, bring about. Clements implies this, but unfortunately some statements that occur here and there, in his *Plant Succession*, e.g. at p. 99: "... a climax is *permanent* because of its *entire harmony* with a *stable habitat*" (italics mine), when isolated from their context and from the author's general concepts regarding the climax, are marked causes of misunderstanding that I have had to explain to more than one ecologist, either prospective or trained. In this respect, it is worth while referring to Cowles's (1901, p. 81) reminder that a condition of stable equilibrium can never actually be reached, since we have a variable, the community, approaching another variable, the habitat. Braun-Blanquet (1932, p. 322), perhaps, has expressed the idea of dynamic balance somewhat hyperbolically in saying that the climax is only a resting point, "a breathing space in the ceaseless change of the composition of vegetation." We must remember, too, that the influence of factors of change alter, too, as the sere develops, as the climax adjusts itself from stage to stage, from efficiency to greater efficiency. Yapp (1925, p. 705) has explained, rightly, that the influence of "indirect biotic factors" (biotic reactions in the sense of Clements and myself), becomes more and more marked, that of the *edaphic* and *climatic* factors relatively less, although climate still exercises general control.

(6) The climax may often show a veritable mosaic of "types" depending upon such features as soil types—acting chiefly through the water of the soil—and aspects; i.e. there may be present in great *climaxes* coarser mosaics of *faciations* depending upon climatic variations, in smaller climaxes finer mosaics of *lociations* and *serations* regulated by lesser climatic and by edaphic variations

respectively; the seral communities may show *facies* and *locies* and *serations*. Monotonous uniformity throughout a climax—especially a great climax—must not be expected, more especially since the advent of man. Clements has done a splendid service by emphasising the possibility, indeed the strong probability, of variation. It must be stressed, again, however, that biotic reactions and climate regulate these variations to a much greater extent than does the soil.

(7) Viewed in its natural setting, the climax is not a *plant climax*, although we use and speak of such an abstraction for the sake of convenience: the *climax* is *biotic*, animals no less than plants playing their part. Its full meaning should be implied in the use of the term climax.

(8) The climax is the fundamental unit of vegetation, the fundamental unit, too, for the classification of biotic communities. Clements (1916, p. 177), in stressing the fundamental nature of the climax in classification as well as in all successional and developmental studies, has done ecology a signal service. Recognition of climaxes, he points out, is still a matter of some difficulty, owing to our natural lack of information; though this situation must of course improve with time and experience. Hence we should be able to achieve an ever increasing efficiency in the study and use of this fundamental unit. Warming and Graebner (1933, p. 400), however, in their last work, were still definitely of the opinion that the dynamic, genetic basis of the study of plant communities could not be used as a basis for a systematic classification. Gams (1918), and Saxton (1922, 1924) believe that the *synusia* is preferable to the *association* (in the sense of the English school of ecologists): this I find difficult to understand in the light of the fundamental nature of the climax.

It is essential to stress, in passing, although the matter will receive fuller attention in Part III of this communication, that the utility of the climax in Clements's sense would be greatly impaired were we to attempt to isolate from it the concept of the community as a *complex organism*.

Its natural, dynamic utility for orientation of research in *succession*, *development*, and *classification* would be distinctly diminished. Cooper (1926, pp. 409–10) is of the contrary opinion: the utility of the climax as a fundamental basis for classification does not necessarily depend upon the close identification of community and organism.

(9) While instances of *climax-retardation* are commonly known wherever climax studies have been attempted, our knowledge of *climax-acceleration*—through *succession-acceleration*—is still somewhat limited. Causes acting in the direction of *biotic reaction*—such as fire, grazing, drainage, and irrigation among others—are able to bring about more rapid attainment of climax conditions. In this respect, the study of the development of dense thorn and other scrub upon over-grazed, fire-free grass-veld in South and East Africa is of great importance.

(10) Now that ecology is being applied to an ever extending degree in the practices of agriculture, pasture management, and forestry, it is increasingly

plain that a knowledge of the phenomena of the climax, and its relatives the proclimax, and the subclimax in their various forms, is demanded of workers in these applied aspects of biology.

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(To be concluded.)

REVIEWS

The Life Forms of Plants and Statistical Plant Geography. Being the collected papers of **C. Raunkiaer**, translated into English by **H. Gilbert-Carter**, **A. G. Tansley** and **Miss Fausbøll**. 9½ by 6¼ inches; pp. xvi + 632, with 189 photographs and figures. Clarendon Press, Oxford. Price 30s. 1934.

This volume is a mark of the esteem in which Prof. Raunkiaer is held by his botanical compatriots and the outcome of their very praiseworthy desire that his writings should be more widely known. These writings were published originally as papers in various Danish periodicals or as books. One, the last, appears here for the first time. The wish of the Danish committee was that they should be brought together in one volume in English translation. The work has been well done. The translators are to be congratulated on an easy readability, and the Clarendon Press on a most pleasing format. It is good to realise that Prof. Raunkiaer lives to see his writings collected in this way and rendered accessible to a much wider botanical public than hitherto.

The papers fall into two main classes, dealing respectively with life forms and with the precise description of plant communities. There are also briefer papers, of less permanent value, on the nitrate content of *Anemone nemorosa* in different habitats, and on the effect of vegetation on soil acidity.

A large part of the book deals with the subject which is so intimately associated with Raunkiaer's name, the Life Forms of plants. Raunkiaer's original publication on this subject appeared in 1904, and a brief summary was given by W. G. Smith in Vol. 1 of this *Journal*. For the first time Raunkiaer's own account of his great scheme is available for English readers. One is impressed by the steady certain tread of his exposition, by the beauty of the illustrative drawings by Mme Raunkiaer, by the emergence of the four major "biological climates", by the interest of that leisurely tracing of the chamaephyte biochores and by the delight of finding their correspondence with July isotherms. One is reminded frequently enough that the author has his mind on the facts as well as on his theories: there is much labour involved in the determination of life forms, nor are they clearly divisible categories.

The justification for Raunkiaer's choice of the position of perennating buds as a basis for his biological classification lies in the successful application of the resulting system. The steady change in the numerical proportions of the types with change in climate amounts to an abundant justification. Difficulties and doubts occur to one's mind, however. There is the familiar fact that the life form of the dominant species is frequently not the characteristic life form of that biological climate. Thus evergreen and deciduous phanerophytes dominate regions in Europe which belong to the therophyte and hemicryptophyte climates. It is evident that features of special morphology and physiology of the sort that determine, for instance, resistance to drought and cold are playing a part which permits a certain favoured few amongst the bulkier life forms to flourish outside their real home. It can be surmised, indeed, that continued evolution of Angiosperms would lead to a shifting of the maxima of the various biological spectra towards the phanerophyte end. Raunkiaer adopts the attitude that the biological climate should be defined by the biological spectrum, and that physiognomy should be the basis only for further subdivision. This is a tenable view, but it is not clear that it has advantages over the physiognomic methods of classification, which are so much easier of application. In fact a strong case can be made for a primary physiognomic classification and the use of life form spectra for purposes of detailed description. Despite Raunkiaer's assertions to the contrary, succession does play an important part in determining

the relative proportions of the life form classes. His own data show a marked preponderance of therophytes on sand-dunes and young salt-marshes, and of chamaephytes on heaths in a hemicryptophyte climate where the ultimate dominants are phanerophytes. Counts on the data for chalk escarpment grassland (Tansley and Adamson) and for beechwoods on chalk (Watt) show the following spectra:

	Ph.	Ch.	H.	G.	Th.
Grassland %	0	5	72	11	12
Beechwood %	23	7	56	15	0

Both are spectra of a hemicryptophyte climate, it is true, but it is evident that the tracing of a biochore in a region where the vegetation is at various stages of succession, primary or deflected, will be a more tentative matter than in the Arctic. Data leading to the same conclusion are given by Watt in a recent paper in this Journal. He is comparing successional woodland communities on the South Down's plateau with mature beechwoods of the same seres, and shows an interesting change in the relative proportions of scapose and caespitose hemicryptophytes:

	Ash-oakwood	Beechwood
Hemicryptophyta caespitosa %	12	23.5
Hemicryptophyta scaposa %	39	16.5

Two other points arise from these and accompanying data: that the subdivision of Raunkiaer's classes as proposed by Braun-Blanquet may have considerable value, and that the successional changes in biological spectra may be correlated with significant environmental change, here a soil deterioration which seems in this country to be bound up with the dominance of beech. The inference is still, however, that the chief value of the classes, at present at any rate, lies in the further, more detailed, exploration of the ecological system rather than in its preliminary definition, which can more profitably be in terms of physiognomy and floristic. For the purpose of this further exploration it should be a matter of ecological routine to determine the spectra not only of all the species present in a community but also of the "characteristic" or "significant" species, if these terms can ever be satisfactorily defined.

Raunkiaer uses as a basis for the delimitation of his biological climates the "normal" spectrum of a thousand species selected at random from Index Kewensis. The mode of selection gives over-representation of tropical types because of their numerical preponderance in the world's flora, and so weights the spectrum heavily in favour of phanerophytes. It is difficult, admittedly, to suggest a practicable alternative method of selection and, as a matter of fact, it is as unnecessary to know the normal spectrum before drawing biochores as to know average temperatures of the world before drawing isotherms. It raises, however, an interesting problem in biological statistics.

The second large group of investigations deals with the use of quantitative methods in ecological research. Here Raunkiaer's chief contributions are the so-called "frequency" method of estimating density, and his Law of Frequencies. His primary aim was the precise characterisation of plant communities, as a step towards the final goal of ecology, "the explanation of the way in which each plant species behaves" in the community. Adequate precision can only be secured by substituting quantitative for qualitative description. The estimation of densities is one of the important problems. Subjective estimates—abundant, occasional, rare—are not good enough: actual counting is too laborious because sampling errors necessitate covering so large an area. The recording of presence or absence of species within each of a large number, fifty or a hundred, of small areas, should give "frequency" determinations having a close relation to actual densities, but with only a fraction of the labour. Raunkiaer experimented persistently and satisfied himself that the most useful area was 0.1 sq. metre. A species has, then, a frequency of 44 if it occurs in 44 per cent. of quadrats, 0.1 sq. metre in area, located at random in the community under investigation.

It is easy to show theoretically that, if individuals of a species are distributed at random, the relation between frequency, in Raunkiaer's sense, and real density, is logarithmic. But it can also be shown, experimentally, that plants are not distributed at random, so that the form of the relation cannot, in fact, be predicted. It is hopeless, then, to get an accurate estimate of density from frequency data. This does not, however, completely destroy the value of such data. They are undoubtedly giving information of a higher precision than the subjective estimates, and combined with notes on the physiognomy of the community they provide a very valuable descriptive method. It is evidently desirable, however, to have a standard size of quadrat for frequency estimations, since results with one size cannot be translated into terms of a different size.

The Raunkiaer Law of Frequencies has been much discussed of late. The "law" expresses the fact that, over a fair range of quadrat size, the species of a community tend to have either low or high frequencies, relatively few occurring in the central frequency classes. The occurrence of two maxima is to be expected on theoretical grounds if certain plausible assumptions are made about the distribution of individuals of a species; that is, the "law" is to that extent merely a statistical truth rather than an ecological phenomenon. The statisticians do not, however, provide a satisfactory explanation of the *position* of the second maximum, which seems to arise from the high "invasion pressure" of the species which establish themselves in the most frequent environments within the limits of the community. There is thus a cumulative effect of dominance, leading to the covering of a greater area by the dominant species than their habitat preferences would explain, and thus to a higher frequency than would be expected.

In reading through these papers dealing with the use of his quantitative methods one cannot fail to be impressed by the enormous amount of field work which Raunkiaer has done. The work is primarily descriptive, and the immediate object twofold: to preserve at least an accurate description of the rapidly vanishing natural vegetation of Denmark, and to "investigate and describe the plant communities in such a way that the results can be used for exact comparative treatment of plant communities in different regions and with different floristic compositions". The second is the chief scientific aim, and is a necessary step towards understanding why plants grow where they do. The papers constantly remind us that plant communities are not sharply defined entities, that their limits are arbitrarily set, and that their classification is not yet an expedient end in itself. There is therefore no elaborate hierarchy of units, and the formation has an elastic definition. It is merely a community which it is convenient to delimit for purposes of description and analysis. These papers will prove a useful corrective to ecological literature which is not so firmly tied to "stubborn and irreducible facts".

A. R. CLAPHAM.

THE JOURNAL OF ANIMAL ECOLOGY

(VOL. 3, NO. 2, NOVEMBER 1934)

THIS number contains 12 original papers, 2 short notes, 4 reviews and 110 notices of British publications on animal ecology (of which a duplicate set is supplied for use on index cards). There are several ecological survey papers. C. Diver and R. D'O. Good outline the progress of their plan for surveying South Haven Peninsula (Studland Heath) in Dorset; J. G. Myers lists the insects, spiders and false scorpions of a rice ship trading between Burma and the West Indies; G. L. R. Hancock describes a careful survey of the mosquitoes found in different zones of a swamp in Uganda, and proves that at a certain stage in reclamation of swamp malaria mosquitoes become temporarily numerous; A. Roebuck gives a general account of the insect pests of a willow bed in Leicestershire. The last paper forms the background for a six-year statistical and experimental study by H. F. Barnes of gall-midges

(*Rhabdophaga heterobia*) on basket-willows, with special reference to fluctuations in numbers of host and parasites.

Population studies receive much attention. T. Warwick publishes maps of the past and present distribution of muskrats (*Fiber zibethicus*) in the British Isles, which show the spread after introduction during recent years, and the checking of this progress by intensive trapping campaigns. T. H. S. Harrison and J. N. S. Buchan describe their intensive field study of the St Kilda wren (*Troglodytes t. hirtensis*) and put forward interesting observations on differential territories in the two sexes, together with estimates of the population and other ecological notes. B. J. Marples gives maps of the winter starling roosts recorded during a national enquiry in 1932-3, and discusses the relation of the roosts to ecological conditions. Fluctuations in populations are discussed by A. D. Middleton in a paper on game birds and animals, based on shooting-bag records from various estates; and by G. M. Findlay and A. D. Middleton, who show that voles (*Microtus*) probably died from brain infections caused by *Toxoplasma* in North Wales and Argyll in the spring of 1933. J. MacLeod gives the results of experiments proving that sheep ticks (*Ixodes ricinus*) can maintain themselves in nature on wild animals and birds in the absence of domestic animals. Laboratory experiments on the competition relations of two species of *Paramecium* are recorded by Russian workers, G. F. Gause, O. K. Nastukova and W. A. Alpatov.

Notes deal with bird ecology in Tanganyika, and a possible case of rabbit syphilis infection in man. There are reviews of the *Journal of Ecology*, of a book on termites ("white ants"), of a Government report on North Sea cod, and of an American monograph on wild deer.

C. S. ELTON.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT BANGOR, NORTH WALES,
SEPTEMBER 1ST-4TH, 1934.

At the kind invitation of Prof. Thoday the Summer Excursion of the Society was held in Bangor on September 1st-4th. The local organisation was in the hands of Dr Norman Woodhead, who, together with Dr R. Alun Roberts, conducted the excursions. We were fortunate also in having the guidance of Prof. G. W. Robinson, who demonstrated the local soils, and of Dr T. Thomson, who showed us the plantations of the Forestry Commissioners. Three of the days were spent in excursions to different parts of the Snowdonian mountains and the fourth day was occupied by a visit to Anglesey.

Saturday, September 1st. The first excursion was a visit to Cwm Idwal. Here Dr Alun Roberts interpreted for us some of the complexities controlling the development of mountain pastures, pointing out the comparatively recent introduction of sheep grazing into Wales. Sheep were introduced about the middle of the sixteenth century, but were for long afterwards grazed together with cattle. Intensive sheep grazing only dates from 1850 and the type of sheep grazing has been much altered since the beginning of the present century by the rise of the early fat lamb industry. Before the rise of the fat lamb industry old wethers grazed the pastures all the year round, in spring attacking the *Molinia* and *Nardus* tussocks, keeping the mat development down. There is now no grazing from October to April; ewes carrying lambs make much more severe mineral demands on the soil so that there has been a marked deterioration of the mountain pastures. *Nardus* and *Molinia* have extended at the expense of *Festuca ovina*, *Agrostis* and *Anthoxanthum*, and the sheep-carrying capacity of the hills has much diminished. There is also a general tendency for the *Festuca-Agrostis* community to spread in the dry summers and to retrogress after wet ones. The tendency towards deterioration of the pasture and spread of *Nardus* and *Molinia* has been assisted also by the diminution of artificial drainage and clearing.

In the Cwm itself, especially where there were calcareous bands in the Ordovician strata, the party encountered some of the characteristic alpine species of the district, such as *Sedum roseum*, *Thalictrum alpinum* and *Meconopsis cambrica*. On the return journey Dr Woodhead called attention to the flora of the Cwm's extensive peat deposits bordering Llyn Idwal, which had been examined micro- and macroscopically by himself and Dr Hodgson.

On the evening of the same day the excursion party was entertained at a soirée in the Department of Botany and Mr Jackson also showed the new Department of Zoology to interested members. Prof. Robinson gave an informal and most enjoyable lecture on the classification of the soils of North Wales, describing the members of the two major suites of soils employed for survey purposes. The Powys suite consists of soils derived from non-calcareous sedimentary rocks, and the Bangor suite of soils deriving from acidic parent rock. In each suite there are five series containing respectively well-drained shallow soils, well-drained deep soils, soils with impeded drainage, alluvial soils and podsols. Broadly speaking, all these soils fall into the podsol, glei and brown earth soil types. The general climatic conditions tend everywhere towards podsolisation.

Exhibits in the Botanical Department included samples of diatomaceous silts from the Conway Valley, peat samples from the submerged forest of the North Wales coast and from Cwm Idwal, produced by Mr L. M. Hodgson. Dr Woodhead showed a demonstration of the plankton cycle in Llyn Malleg, Anglesey. There was also a large herbarium exhibit of all the arctic-alpine species of the district, and lantern slides of the extensive sand dune and marsh area of Newborough Warren. Other interesting herbarium specimens from Norway and South Africa were shown by Prof. Thoday, who also produced a living flowering specimen of *Stapelia nobilis*, a carrion flower obtained originally from an island in the Victoria Falls.

Exhibits were also shown of Green Fly aphides infecting the potato crop and microscopic preparations of Collembola of North Wales, especially in relation to their distribution on acid and basic soils and the economic importance of some of them as pests.

Sunday, September 2nd. The party visited Cwm Glas and *en route* Dr Alun Roberts demonstrated the multiplicity of tiny small-holdings scattered throughout the quarry districts and said that these were due to squatting in the eighteenth century. In Cwm Glas still more of the characteristic alpine plants were recognised: *Saxifraga oppositifolia*, *S. borealis*, *Asplenium viride*, *Silene acaulis*, *Antennaria dioica*, *Arenaria verna*, *Thalictrum alpinum*, *Polystichum lonchitis*, *Alchemilla alpestris*. In the upper and lower lakes of the Cwm were also found the interesting and characteristic aquatic species *Lobelia Dortmanna*, *Subularia aquatica*, *Littorella uniflora* and *Isoetes lacustris*.

Monday, September 3rd. The party proceeded by bus to Newborough Warren and were able to see villagers in Newborough making mats and ropes out of Marram Grass, which is still regularly cut from the dunes. The ropes are used for some kinds of plumbing and the mats for covering haystacks and glass frames. The Warren itself is an extremely extensive area of magnificent mobile *Psamma* dunes with secondary *Salix* dunes behind them, and encloses numerous large dune slacks: these at the time of the visit were quite exceptionally dry and had been subjected to strong rabbit attack. In the slacks were found abundant *Selaginella spinosa*, *Gentiana Amarella*, *Riccia crystallina*, *Equisetum variegatum*, and on the dunes *Euphorbia Paralias*, *Viola Curtisii* and large stretches of *Rosa spinosissima* and *Rubus caesius*, both suffering considerably from the prolonged drought. At the inn at Llangefni the party enjoyed a peculiarly excellent, varied and abundant tea.

On the return journey Dr Alun Roberts and Prof. Robinson demonstrated the Lledwedjin fattening pastures; these are among the best in Britain and occupied the deep red or brown limestone soil derived from the underlying Carboniferous limestone. There is no calcium carbonate in the soil but a very high base content. There is no podsolisation or formation of a clear profile.

Tuesday, September 4th. Before the excursion Dr Alun Roberts demonstrated to the party the contents of the Museum of articles of ancient husbandry, which he has been getting together in the Department of Agriculture. He showed an extremely interesting series of tools now no longer in use, such as an iron-shod wooden spade of the sixteenth century, an ox-yoke as used in the eighteenth century, turfing irons used for paring off the surface of heath peat for burning, peat-cutting tools, a wooden ridging plough used as recently as 1826, and he also showed the tools used for gorse bruising, pointing out that on the Welsh mountains the common gorse (*Ulex europaeus*) had been introduced by seed from Ireland and that it played a very important part as a winter protein food before the introduction of artificial cake. He also showed the shoes with which cattle were shod to be driven into London. A pallet woven of *Scirpus lacustris* and a very large number of similar articles, all with quite evident historico-ecological implications.

The excursion for the day was to the Forest Commission plantations at Rhyd Ddu. These were demonstrated to us by Dr T. Thomson, Head of the Department of Forestry. He explained that the chief difficulties of establishing woodland in these areas lie in the waterlogging, the low mineral content and the unavailable condition of the nitrogen. He demonstrated the Belgian system of turf planting, which had been employed in combination with the cutting of drainage channels. The turves taken from the drains are inverted and in the hillocks so formed the seedling trees are planted. Here they are initially out of reach of the water-table and benefit from the aeration and weathering of the exposed peat block. Various species of conifers had been planted in this way and some had been subjected to manurial experiments. The most successful species were Sitka and Norway Spruce, and Dr Thomson pointed out that the Sitka Spruce is native of the oceanic climate of the northern part of the west coast of North America, where climatic conditions might be said to resemble to some

extent those of North Wales. In all the plantations there was visible the most striking degree of correlation of tree growth with soil drainage, which latter factor was also demonstrated by the distribution of *Calluna*.

In all about twenty-five visiting members took part in the meeting and we were shown throughout the greatest hospitality. At the close of the last excursion Prof. Tansley expressed the very cordial thanks of the party to our kind hosts and guides, and to these the Secretary would add the sincere appreciation of the Society as a whole.

ANNUAL MEETING AT UNIVERSITY COLLEGE, LONDON JANUARY, 4TH-5TH, 1935.

SOIRÉE IN THE DEPARTMENT OF BOTANY.

Members and guests were entertained at a soirée in the Department of Botany, University College, on the evening of Friday, January 4th, and about ninety members and visitors were present.

An interesting series of exhibits had been set out dealing particularly with various aspects of Plant Ecology. Dr C. E. Hubbard and Mr F. Ballard showed a large number of interesting herbarium specimens illustrating seed dispersal in the Gramineae, and Prof. Salisbury showed preparations illustrating unsuspected seed dispersal mechanisms in *Bidens tripartita* and *Plantago Coronopus*. Mr Marsden Jones and Dr Turrill illustrated a wide range of sex types in *Ranunculus acris*. Prof. Salisbury showed also a series of lantern slides illustrating the vegetation of drying mud, a vegetation often influenced remarkably by the germination of dormant seeds forced into activity by drying. Prof. Salisbury also produced exhibits showing effects of competition between different species of *Hypericum*, where very different degrees of root development in allied species appear to offer explanations of survival and disappearance. Dr F. W. Jahe showed exhibits illustrating the relationship of wood anatomy to the sclerophyll or deciduous habit of the genus *Quercus*, and with Dr Salisbury identified charcoal samples from prehistoric sites. An extremely interesting series of drawings of specimens illustrating the seedling development of *Limosella aquatica* was shown by Miss R. Dowling. Dr Jahe and Dr B. Russell Wells produced an exhibit illustrating germination and seedling development of *Utricularia vulgaris*.

The thanks of the Society are due to Prof. Salisbury and the Staff of his Department for having arranged this very interesting series of exhibits.

THE ANNUAL MEETING.

The twenty-first annual meeting of the Society was held in the Department of Botany, University College, London, on the following morning, Saturday, January 5th, at 10.30 a.m., the President, Prof. J. R. Matthews, occupying the Chair. The minutes of the previous meeting were read and confirmed. The report of the Honorary Secretary was then read and adopted.

HON. SECRETARY'S REPORT FOR THE YEAR 1934.

The Twentieth Annual Meeting of the Society was held in the Botany School, Cambridge, on January 3rd, 1934. At a soirée given on the previous evening about ninety members and guests were present and a wide range of exhibits was shown. The cordial thanks of the Society are due to Prof. Seward for allowing the use of his Department and for facilitating arrangements for the meeting.

Following a kind invitation from Prof. Thoday, the Summer Meeting of the Society was held at Bangor, North Wales, from Friday, August 31st to Wednesday, September 5th. It was attended by about twenty-five visiting members. The excursions were conducted by Dr

N. Woodhead and Dr R. Alun Roberts, and we were fortunate in having the competent help of Prof. G. W. Robinson to demonstrate the local soils, and of Dr T. Thomson to show us the experimental plantations of the Forestry Commissioners. Three days were occupied in very pleasurable visits to Cwm Idwal, Cwm Glas and Rhydd Ddu in the Snowdonian Massif (of which a fuller account will be found on pp. 251-3). The excursion party were shown a wide range of mountain vegetation, as a rule intricately distributed under the control of such factors as slope, aspect, drainage, altitude, parent rock and varying types and intensities of grazing. The party saw also a considerable number of the alpine species characteristic of the district. A fourth day was occupied in visiting the extensive sand-dune area of Newborough Warren on the coast of Anglesea. On the second evening of the meeting a soirée was given in the Department of Botany. Prof. Robinson gave an informal lecture on the soils of North Wales and Mr Jackson showed the new Zoological Department to interested members of the party. Throughout the meeting we were shown the greatest hospitality, Prof. and Mrs Robinson even suffering their home to be invaded by a riotous evening party for all the members of the excursion. Our most cordial thanks are due to our hosts and guides for their kindness, and especially to Dr Woodhead, who competently shouldered all the work of the local organisation, and to Prof. and Mrs Thoday, who had specially returned from Norway to entertain us in Bangor.

In the past year two numbers of Vol. III of the *Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 128 and 160 pages, which is about the size of Vol. II. The published material included twenty-one original articles with thirteen plates, in addition to notes, notices and reviews. Mr Elton has now adopted the original and useful device of reprinting the Notices of Publications on Animal Ecology in a separate form suitable for direct incorporation into card-index systems. These reprints are issued free with the *Journal of Animal Ecology* and can also be purchased separately. In the past year there has been an increase in the numbers both of members and non-members of the Society who take the *Journal of Animal Ecology*, so that at its present size it is now paying its way.

Since the last Annual Meeting there have been issued two numbers of the *Journal of Ecology*, appearing in February and August, and containing 577 pages and forty-one plates. This includes twenty-three original papers as well as letters, notes and reviews. This, the twenty-second volume of the *Journal*, is the largest which has yet been produced but the editor nevertheless reports very severe pressure upon the space available.

The Society's transplant experiments at Potterne are continuing to give satisfactory results in the hands of Mr Marsden-Jones and Dr Turrill.

Since the end of last year the membership of the Society has risen from 322 to 331: there have been twenty-two new members elected and thirteen members have resigned or died. We regret especially to record the death of Dr Leonard Cockayne, F.R.S., one of the outstanding figures in modern work on vegetation. Dr Cockayne was made an honorary life-member of the Society only at the last Annual Meeting. Of the present membership list, 191 members receive the *Journal of Ecology* alone, 84 the *Journal of Animal Ecology* alone, and 52 receive both journals. The changes from the corresponding figures of last year are respectively nothing, plus four, and plus two.

The Honorary Treasurer presented the accounts and balance sheet of the Society, which were adopted subject to audit. It was proposed from the Chair and carried *nem. con.* that Messrs William Norman and Son, Chartered Accountants, be reappointed auditors to the Society. Mr C. Oldham proposed a vote of thanks to Mr Boyd Watt for kindly continuing his treasurership of the Society, and this was carried unanimously.

The Secretary gave notice that the Council proposed in the ensuing year to revise the Rules of the Society, and asked members who desired to see alterations in the Rules to communicate their wishes or ideas to the Council.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR YEAR ENDING 31ST DECEMBER, 1934

Income

	£	s.	d.	£	s.	d.
Subscriptions received including arrears ...	341	18	7			
less prepayments for 1935-6 ...	23	4	0			
Interest: On Investments ...	34	10	0	318	14	7
On Deposit Account ...	18	5				
<i>Journal of Ecology</i> —Sales, etc.: Current volume xxii, 1934 ...	447	18	0			
Back volumes and parts ...	71	3	10			
Contribution for illustrations ...	30	0	0	549	1	10
Index Volume, <i>Journal of Ecology</i> (vols. i-xx)— Sales ...				26	19	2
<i>Journal of Animal Ecology</i> —Sales, etc. Vol. iii, 1934: Subscriptions received ...	161	0	0			
Grant from Royal Society in 1933 ...	50	0	0			
Sales ...	148	14	5			
Sales of reprints ...	32	18	0			
Contributions re publication ...	25	0	0			
Vols. i and ii: Sales of back numbers ...	50	11	8	458	4	7

£1388 8 7

BALANCE SHEET AT 31ST DECEMBER, 1934

Liabilities

	£	s.	d.	£	s.	d.
Membership subscriptions, prepaid for 1935-6 ...				23	4	0
<i>General Revenue Account</i> — <i>Balance of Funds</i> : Balance at 31st December, 1933 ...	1030	19	5			
less Sales overestimated in 1933 (<i>A/c Journal of Animal Ecology</i>) ...	120	0	0			
<i>Add</i> Surplus at 31st December, 1934 ...	910	19	5			
	82	8	1	993	7	6

£1016 11 6

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.
(Signed) WM. NORMAN & SONS,
Chartered Accountants.

120, BISHOPSFOGATE, LONDON, E.C. 2.

Expenditure

	£	s.	d.	£	s.	d.
<i>Working Expenses</i> : Printing Circulars, Duplicator, etc. ...				4	10	6
Postages, etc. ...	12	4	0			
Bank Charges ...				4	4	4
Clerical Assistance (Secretary and Treasurer) ...	15	0	0			
Audit Fee ...				31	18	10
B.E. Society's Transplant Experiments Fund Grant ...				3	3	0
<i>Source Expenses</i> : <i>Journal of Ecology</i> , vol. xxii, 1934: ...				5	0	0
Paper, Printing, Illustration, etc. ...				6	9	0
Binding ...				632	14	2
Postage, etc. ...				10	6	
Publishers' Commission ...				44	15	5
Index Volume, <i>Journal of Ecology</i> (vols. i-xx): ...				76	0	2
Sundry Expenses ...						
<i>Journal of Animal Ecology</i> , vol. iii, 1934: ...				7	0	6
Paper, Printing, Illustration, etc. ...				383	5	4
Publishers' Commission ...				36	1	7
Carriage, Insurance, Advertising, etc. ...				19	2	0
<i>Balance</i> —Surplus for the year ...				438	8	11
				1306	0	6
				82	8	1
				£1388	8	7

Assets

	£	s.	d.	£	s.	d.
<i>Westminster Bank</i> — <i>Credit Balances</i> : Current Account ...				18	6	
Deposit Account ...	100	0	0			
<i>Investments</i> : £700 34 % War Loan at cost ...				717	3	0
(Market value at 31st December, 1934, at 109, £713. 0s. 0d.)						
£200 3 % Conversion Loan at cost ...				198	10	0
(Market value at 31st December, 1934, at 124, £248. 0s. 0d.)						
				915	13	0
				£1016	11	6

NOTE. A further Asset is the unsold stock of the *Journals* and Index Volumes held for the Society by the Publishers.

(Signed) HUGH DAVY W. COOK

The Meeting proceeded to the election of Officers as follows:

Vice-President: DR E. S. RUSSELL.

Council Members: DR W. H. PEARSALL and DR R. GURNEY.

Hon. Editor of the Journal of Ecology: PROF. A. G. TANSLEY.

Hon. Editor of the Journal of Animal Ecology: MR C. S. ELTON.

Hon. Treasurer: MR H. BOYD WATT.

Hon. Secretary: DR H. GODWIN.

It was proposed from the Chair and carried *nem. con.* that a grant of five pounds should be made towards the expenses of the Society's transplant experiments in the year 1935.

Prof. Matthews then proceeded to give his extremely stimulating presidential address on "Geographical relationships of the British Flora".

After the adjournment for lunch the meeting resumed with a report by Dr Turrill on the progress of the Society's transplant experiments at Potterne. Dr Turrill reported that his work with Dr Marsden Jones on these experiments had now extended over seven seasons and that a third report on the results was ready for publication in the *Journal*. He reported the successful establishment of *Fragaria vesca* and *Phleum pratense* (diploid and hexaploid) in place of the *Silene vulgaris* and *Silene maritima*, which formerly had a place in the beds, and on which all the information likely to be obtainable had now been recorded. Dr Turrill gave a general account of the varying types of change recorded in morphology, flowering, fruiting, vegetative growth, etc. induced by the different types of soil employed experimentally.

Mr V. J. Chapman gave an account of the air and water movements in salt marsh soils, basing his description particularly on work done on the salt marshes at Scolt Head, Norfolk. He distinguished clearly between the processes involved in the access of water to a salt marsh and in those involved in its removal after flooding at high tide. During the period of rising tide, as water flows into the channels and creeks, lateral seepage takes place through the banks and causes a rise in the water-table of the marsh. Finally, the rising tide causes complete superficial flooding of the marsh. Mr Chapman gave a convincing account of experiments and observations which demonstrated that throughout such a period there remains enclosed in and below the surface mud of the marsh a permanent gas phase. This aerated layer is largely due to the cavities formed by decaying roots of salt marsh plants and Mr Chapman showed that living roots of the marsh vegetation are very largely confined to this aerated layer. In the discussion which followed Prof. T. G. Hill, Dr Godwin and Mr Steers took part.

Mr A. D. Middleton read a paper on the influence of adverse factors on the population of partridges (*Perdix perdix*). By using extensive statistics from well-managed estates, together with his personal observations, Mr Middleton was able to trace the fate of the partridge broods through the whole of the year. He estimated that 23 per cent. of the nests are destroyed by foxes, rooks, or the accidents of cultivation, and other minor causes. The fertility of the eggs was quite high, about 94 per cent. hatching out. He demonstrated that of an average brood of fifteen only about five birds reach maturity, and on most estates about 50 per cent. of those reaching maturity, *plus* the parents, are shot. After shooting there is a large winter wastage, probably due to disease and migration, bringing the final number of birds back almost exactly to the original population size. Mr Elton and Dr Hare took part in the discussion which followed.

Dr C. E. Hubbard gave a short account of some of the vegetation types of Queensland, Australia, illustrating his account with his own very beautiful lantern slides. The following types of vegetation were illustrated—open semi-desert, scrub, *Eucalyptus* forest (very largely cleared now for grazing, pine-apple and banana growing), and rain forest. These communities illustrated response to an extremely wide range of climate and soil.

At the close of the meeting the President expressed the cordial thanks of the Society to Profs. Salisbury and Hill for their hospitality in allowing the meeting to be held in their Department, and particularly to Miss Dowling and the rest of the staff, who had so competently cared for the entertainment of their guests.

LIST OF MEMBERS (JANUARY 23rd, 1935)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

- E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
- E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
- A. **Alexander**, W. B., M.A.; University Museum, Oxford.
- E. **Allan**, Dr H. H.; Plant Research Institute, Palmerston North, N.Z.
- A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
- E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
- E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
- E. **Alvarez-Laviada**, Prof. M. M.; Estación Navanjerade Levante, Burjasot (Valencia), Spain.
- E. A. **Amory**, C.; 1811, Q Street, Washington, U.S.A.
- E. **Anand**, P. L., M.Sc.; c/o Messrs Grindlay and Co., 54, Parliament Street, London.
- E. **Andersonian Naturalists' Society** (cf. Glasgow).
- E. **Andreànszky**, Baron Gábor; Budapest, VIII, Múzeum-Körür 4, Hungary.
- E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
- E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
- E. **Ashby**, Eric, B.Sc.; Imperial College of Science, London, S.W. 7.
- E. **Bacon**, Mrs Alice; The Technical College, Brighton.
- E. **Ballard**, F., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew.
- A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
- E. **Barnes**, Dr B.; 28, Torridon Road, London, S.E. 6.
- A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
- E. **Bates**, G. H., B.Sc.; Hill House, King's Lynn, Norfolk.
- E. A. **Beauchamp**, R. S. A., B.A.; The Laboratory, Wray Castle, Ambleside.
- E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
- A. **Bertram**, G. C. L., B.A.; St Keyne, Berkhamsted, Herts.
- E. A. **Bews**, Prof. J. W.; University College, Pietermaritzburg, Natal.
- E. **Bharucha**, Dr F. R.; 6, Alexandra Road, New Gamdevi, Bombay 7.
- A. **Bird**, Prof. R. D., M.Sc., Ph.D.; University of Oklahoma, Norman, Okla., U.S.A.
- E. **Blackburn**, K. B., D.Sc.; Armstrong College, Newcastle-upon-Tyne.
- E. **Blackman**, G. E.; Jeallot's Hill Agricultural Research Station, Wanfield, Berks.
- E. **Blackman**, Prof. V. H., F.R.S.; Imperial College of Science, London, S.W. 7.
- A. **Blair**, H. M. S., M.B., B.S.; 2, Westoe Terrace, S. Shields, Durham.
- E. **Bloomer**, H. H.; Longdown, Sunnysdale Road, Swanage, Dorset.
- E. **Bor**, N. L., M.A., D.Sc.; Charduar, Lokra, P.O., Balipara, Frontier Tract, Darrang, Assam.
- E. **Børgesen**, Dr F. C. E.; Botanisk Museum, Gothersgade 130, Copenhagen.
- E. **Borthwick**, Dr A. W.; 25, Drumsheugh Gardens, Edinburgh.
- E. A. **Boycott**, Prof. A. E., F.R.S.; 17, Loom Lane, Radlett, Herts.
- A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
- E. **Boyd**, L.; Royal Botanic Gardens, Edinburgh.
- E. **Bracher**, Miss Rose, Ph.D.; Dept. of Botany, The University, Bristol.
- A. **Bradley**, P. C. Sylvester; Wantage Hall, Reading.
- E. **Braid**, Major K. W.; 6, Blythswood Square, Glasgow.

- E. **Braun**, Miss E. L.; 2702, May Street, Cincinnati, Ohio, U.S.A.
- E. **Brenchley**, Dr Winifred E.; Rothamsted Experimental Station, Harpenden, Herts.
- E. **Brodsky**, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
- E. **Brooks**, F. T., M.A., F.R.S.; Botany School, Cambridge.
- A. **Brown**, F. M.; 20, Highgrove Road, Copnor, Portsmouth.
- E. **Burnett**, Miss I. M.; Malvern Girls' College, Worcestershire.
- E. **Burt**, B. D.; Botanist, Taetse Research, Shinyanga, Tanganyika Territory, E. Africa.
- E. **Burt Davy**, Dr J.; Imperial Forestry Institute, Oxford.
- E. **Butcher**, R. W., B.Sc.; The Tees Laboratory, Barnard Castle, Co. Durham.
- A. **Buxton**, Prof. P. A.; London School of Hygiene, Keppel Street, London, W.C. 1.
- E. **de Caen**, Mrs. Ph.D.; Springfield, Delgany, Co. Wicklow, Ireland.
- A. **Cameron**, A. E., D.Sc.; Dept. of Agricultural Zoology, The University, Edinburgh.
- A. **Carpenter**, Prof. G. D. Hale, M.B.E., M.D.; Penguella, Hid's Copse Road, Cumnor Hill, Oxford.
- A. **Carpenter**, J. R., M.Sc.; Dept. of Zoology, University of Oklahoma, Norman, Okla., U.S.A.
- A. **Carpenter**, Prof. K. E., Ph.D.; 105, Front Street, Chestertown, Maryland, U.S.A.
- A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
- E. **Carter**, Dr Nellie; E. London College, Mile End Road, London, E. 1.
- E. **Cavers**, Dr F.; Oakfield Avenue, Knebworth, Herts., *Hon. Life Member*.
- E. **Chambers**, Miss W. E., B.Sc.; Innesbrook, Watlington, Oxon.
- A. **Champion**, F. W.; c/o Messrs Grindlay and Co., Post box 93, Bombay, India.
- E. A. **Chapman**, V. J.; The Rectory, Alcester, Warwicks.
- A. **Charlesworth**, R.; 190, Padgate Lane, Warrington.
- A. **Charteris**, Hon. Guy; 24, Oxford Square, London, W. 2.
- E. **Christophersen**, Prof. E.; B.P. Bishop Museum, Honolulu, T.H.
- E. **Clapham**, Dr A. R.; Botanical Dept., The University, Oxford.
- A. **Clegg**, G. H.; Longridge, Delamere, Northwich, Cheshire.
- E. A. **Clements**, Prof. F. E.; Mission Canyon, Santa Barbara, California.
- A. **Cohen**, E.; 86, Major Street, Manchester.
- E. **Colville**, Miss E. G.; Arngomery, Kippen, Stirlingshire, Scotland.
- E. **Conway**, Miss V. M.; 61, De Freville Avenue, Cambridge.
- E. **Cooper**, Prof. W. S.; Dept. of Botany, University of Minnesota, Minneapolis, Minn.
- E. **Cotton**, A. D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A., *Hon. Life Member*.
- E. **Croydon Natural History and Scientific Society**, 27, High Street, Croydon.
- E. **Curtis**, Miss W. M., B.Sc.; 12, Blenheim Road, Caversham, Reading, Berks.
- E. **Cutting**, E. M., M.A.; 125, Tredegar Road, Bow, London, E.
- A. **Dalgety**, C. T.; Denver Hall, Downham Market, Norfolk.
- A. **Darling**, F. F., Ph.D.; Brae House, Dundonnell, by Garve, Wester Ross, Scotland.
- E. **Davey**, Miss A. J., M.Sc.; University College of N. Wales, Bangor, N. Wales.
- E. **Davies**, W. C.; The Cawthron Institute, Nelson, N.Z.
- A. **Davis**, D. H. S.; University Museum, Oxford.
- E. **Dawson**, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorks.
- E. **Deam**, C. C.; Bluffton, Indiana, U.S.A.
- E. **Delf**, Dr E. M.; Westfield College, Hampstead, London, N.W. 3.
- A. **Diver**, C.; 40, Pembroke Square, Kensington, London, W. 8.
- E. **Dowling**, Miss R. E., B.Sc.; The Nest, Ledgers Road, Slough, Bucks.
- A. **Duncan**, A. B., B.A.; Gilchristland, Closeburn, Dumfries.
- E. **Du Rietz**, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
- E. A. **Dyke**, F. M., B.Sc.; Branksome, Boreham Woods, Herts.

- E. **Eden**, T.; Tea Research Institute, St Coombs, Talawakelle, Ceylon.
- E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.
- E. **Eklblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
- A. **Ellis**, R.; 2420, Ridge Road, Berkeley, California, U.S.A.
- E. A. **Elton**, C. S.; Dept. of Zoology, University Museum, Oxford, *Hon. Editor of The Journal of Animal Ecology*.
- E. **Essex Field Club**, The (Essex Museum of Natural History, Romford Road, Stratford, Essex).
- E. **Evans**, E. Price; White Broom, 69, Westgate, Hale, Cheshire.
- E. **Falk**, P.; 24, Bilton Road, Rugby.
- E. **Farmer**, Prof. Sir J. B., F.R.S.; St Leonards, Weston Road, Bath.
- E. A. **Featherly**, Prof. H. I.; Oklahoma Agricultural and Mechanical College, Stillwater, Okla., U.S.A.
- E. **Fenton**, E. Wyllie; 13, George Square, Edinburgh.
- E. **Fisher**, H. S., M.Sc.; University College, Oxford.
- A. **Fisher**, J. M. Mc.; Magdalen College, Oxford.
- E. A. **Fitzgerald**, D. V.; Clamngor Hill, Haslemere, Surrey.
- E. **Foggie**, A., B.Sc.; Assistant Conservator of Forests, Stavros, *via* Polis, Cyprus.
- A. **Ford**, J.; New College, Oxford.
- E. **Fraser**, G. K., M.A., B.Sc.; Forestry Dept., Marischal College, Aberdeen.
- E. **Fredericks**, S. M. D.; c/o 4, Parkway Close, Welwyn Garden City, Herts.
- E. **Fritsch**, Prof. F. E., F.R.S.; Danesmount, Tower Hill, Dorking.
- E. **Fuller**, Prof. G. D.; Botany Dept., The University, Chicago, Ill., U.S.A.
- E. **Gams**, Dr H.; Innsbruck-Hotting, Bauerngasse 15, Austria.
- E. A. **Garner**, J. H., B.Sc.; West Riding Rivers Board, 71, Northgate, Wakefield.
- E. **Gibson**, Miss C. M.; The Municipal College, Portsmouth.
- A. **Gilbert**, H. A., B.A.; Bishopstone, Hereford.
- E. **Gilbert-Carter**, H., M.A., M.B.; Cory Lodge, Botanic Garden, Cambridge.
- E. **Gillman**, H., M.Sc.; District Agricultural Office, Bukoba, Tanganyika Territory.
- E. **Gilmour**, J. S. L., B.A.; Royal Botanic Gardens, Kew, Surrey.
- E. A. **Glasgow and Andersonian Nat. Hist. and Microscopic Soc.**; Societies' Rooms, Royal Technical College, Glasgow.
- E. A. **Godwin**, H., Ph.D.; Botany School, Cambridge, *Hon. Secretary*.
- E. A. **Good**, R. D'O.; University College, Hull.
- E. **Gourlay**, W. B., M.A., M.B.; 7, Millington Road, Cambridge.
- A. **Gross**, Prof. A. O., A.B., Ph.D.; Bowdoin College, Brunswick, Maine, U.S.A.
- E. **Griffith Tedd**, H.; P.O. Box 30, Xanthie, Greece.
- E. A. **Griffiths**, B. M., D.Sc.; Dept. of Botany, University Science Labs., South Road, Durham.
- E. **Gunawardena**, D. C., B.A.; Melbourne House Hotel, Gower Street, London, W.C. 1.
- A. **Gurney**, Dr R.; Bayworth Corner, Boar's Hill, Oxford.
- E. **Halket**, Miss A. C., B.Sc.; Bedford College, Regent's Park, London, N.W. 1.
- E. **Halliday**, W. E. B.; c/o Dominion Forest Service, Customs Building, Winnipeg, Manitoba, Canada.
- E. **Hands**, Mrs; Beachfield, The Folly, Radlett, Herts.
- E. **Hanson**, Dr Herbert C.; Botanist and Head of Dept. of Botany, North Dakota Agric. College and Expt. Station, Fargo, North Dakota, U.S.A.
- A. **Hardy**, Prof. A. C., M.A.; University College, Hull.
- E. **Hare**, C. Leighton, B.Sc.; Greenmount, Cleeve Hill, nr Cheltenham.
- A. **Hare**, Prof. T., M.D.; 70, Holywell Hill, St Albans.
- A. **Harris**, W. V.; Dept. of Agriculture, Morogoro, Tanganyika Territory.
- E. **Harrison**, A. B.; The Hollies, Farndon, Newark-on-Trent.

- A. **Harrisson**, T. H.; Pembroke College, Cambridge.
- E. **Hartley**, P. N.; Westlecot, Loxwood Avenue, Worthing, Sussex.
- A. **Harvey**, A. L., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.
- E. **Heddie**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13, George Square, Edinburgh.
- E. **Hilary**, Miss D., B.Sc.; 15, Plevna Terrace, Bingley, Yorks.
- E. **Hill**, Sir A. W., F.R.S.; Royal Botanic Gardens, Kew, Surrey.
- E. **Hill**, Prof. T. G.; University College, London, W.C. 1.
- A. **Hobby**, B. M.; University Museum, Oxford.
- E. **Holch**, Dr A. E.; Botany Dept., University of Denver, Colorado, U.S.A.
- E. **Hole**, D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.
- E. **Holtum**, R. E., M.A.; The Botanic Gardens, Singapore.
- E. **Howarth**, W. O.; Botany Dept., The University, Manchester.
- E. **Hubbard**, C. E.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- A. **Huntingdon**, E.; Dept. Geological Sciences, 4, Hillhouse Avenue, New Haven, Connecticut, U.S.A.
- E. **Hutchinson**, R. R.; 11, Fryston Avenue, Croydon.
- E. **Hyde**, H. A., M.A.; National Museum of Wales, Cardiff, S. Wales.
- A. **Imms**, D. A., D.Sc.; Zoological Dept., Cambridge.
- A. **Jackson**, C. H. N., Ph.D.; Dept. of Tsetse Research, Shinyanga, Tanganyika Terr.
- E. **Jennings**, A. E.; Carnegie Museum, Pittsburg, Pa., U.S.A.
- E. **Joaquim**, Miss U. I. A., B.Sc.; Woodhall Girls' School, Woodhall Spa, Lincs.
- E. A. **Jones**, Miss G. M.; The Cottage, Wraysbury, Bucks.
- E. **Kashkarov**, Prof. D.; Tashkent, Novaia 19, Usbekistan, U.S.S.R. (Russia).
- E. **Kawada**, Prof.; Forest Experiment Station, Meguro, nr Tokio, Japan.
- E. A. **Kendleigh**, S. C., Ph.D.; Biological Lab., Western Reserve University, Cleveland, Ohio, U.S.A.
- E. **Kessell**, S. L.; Conservator of Forests, Forests Dept., Perth, W. Australia.
- A. **Kitching**, J. A., B.A.; Birkbeck College, Fetter Lane, London, E.C. 4.
- A. **Lack**, D.; Magdalene College, Cambridge.
- E. **Laughton**, F. S.; Assistant Forest Officer, Concordia, Knysna, C.P., S. Africa.
- E. **Lawrence**, E.; N.D.A., Dept. of Agriculture, Zomba, Nyasaland.
- E. **Leach**, W.; The University, Edgbaston, Birmingham.
- A. **Lemon**, F. E.; Royal Society for Protection of Birds, 82, Victoria Street, London, S.W. 1.
- A. **Lewis**, D. J., M.A.; Shenfield Rectory, Brentwood, Essex.
- E. **Lewis**, Prof. F. J.; University of Alberta, Edmonton, Alberta, Canada.
- E. **Lind**, Miss E. M., B.Sc., Ph.D.; The University, Sheffield.
- A. **London Natural History Society**; c/o Mrs Clauchy, 21, Coram Street, London, W.C.1.
- A. **Longstaff**, Dr T. G., M.A., D.M.; Picket Hill, Ringwood, Hants.
- E. A. **Lowndes**, A. G., M.A., F.L.S.; Marlborough College, Wilts.
- E. **Lüdi**, Dr W.; Brunnmattstrasse 70, Bern, Switzerland.
- A. **MacLeod**, J., Ph.D.; Oakmont Cottage, Lesswade, Midlothian.
- E. A. **McBeath**, D. K.; Ballochyle House, Sandbank, Argyllshire.
- E. **McLean**, Prof. R. C.; University College, Cardiff, S. Wales.
- E. **McLuckie**, J., D.Sc.; Dept. of Botany, The University, Sydney, N.S.W.
- E. **Mangham**, Prof. S., M.A.; University College, Southampton.
- A. **Marples**, B. J.; Zoology Dept., Victoria University, Manchester.
- E. **Marquand**, C. V. B., M.A.; Langdale, 46, Hook Rise, Tolworth, Surrey.
- E. **Marsden-Jones**, E. M.; The Potterne Biological Station, nr Devizes, Wilts.

- E. **Martin**, J. D.; Assistant Conservator of Forests, Lusaka, N. Rhodesia.
- E. **Mason**, E. W.; Inglenook, 63, King's Road, Richmond, Surrey.
- E. **Matthews**, Prof. J. R., M.A.; The University, Old Aberdeen, *President*.
 - A. **Meynle**, M.; Hoar Cross, Burton-on-Trent, Staffs.
- E. A. **Michelmores**, A. P. G., B.A.; Saffron Close, Chudleigh, S. Devon.
 - A. **Middleton**, A. D.; University Museum, Oxford.
- E. A. **Middleton**, A. R.; Biological Labs., University of Louisville, Louisville, Kentucky, U.S.A.
 - Miller**, W. B.; Sojourner's Club, Fort Bayard, New Mexico, U.S.A.
- E. A. **Milne-Redhead**, E., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Mohan**, N. P., M.A.; c/o Lloyds Bank, The Mall, Lahore, Punjab, India.
 - A. **Montague**, F. A.; The Secretariat, Dar-es-Salaam, Tanganyika Territory.
 - A. **Montford**, H. M., B.Sc.; Armina, Petersham Road, Richmond, Surrey.
 - A. **Moon**, H. P., B.A.; Moss Dale, Ullswater, Penrith, Cumberland.
- E. **Mooney**, H. F., M.A.; Ranchi, B.N. Railway, India.
- E. A. **Moore**, Barrington; Stone Acre, Corfe, Taunton.
- E. **Murray**, J. M., B.Sc.; 76, Hillview Terrace, Corstorphine, Midlothian.
- E. **Negri**, Prof. Giovanni; R. Istituto Botanico, via Lamarmora 4, Firenze, Italy.
- E. A. **Newman**, Leslie F., M.A.; St Catharine's College, Cambridge.
- E. A. **Newton**, Prof. Lily, M.Sc., Ph.D.; Dept. of Botany, University College of Wales, Aberystwyth, Wales.
- E. **Nichols**, Prof. G. E.; Botany Dept., Yale University, New Haven, Conn., U.S.A.
 - A. **Nichols**, J. E., Ph.D.; Moorfield Cottage, Arthington, nr Leeds.
 - A. **Nicholson**, E. M.; 58, Petty France, London, S.W. 1.
- E. A. **Nurse**, H. P.; 13, Haggard Road, Twickenham, Middlesex.
- E. **Ogg**, W. G., M.A., Ph.D.; Macaulay Inst. for Soil Research, Craigiebuckler, Aberdeen.
- E. A. **Oldham**, Charles; The Bollin, Shrublands Road, Berkhamsted, Herts, *Vice-President*.
- E. **Oliver**, Prof. F. W., F.R.S.; Egyptian University, Abbassia, Cairo, Egypt.
- E. A. **Oliver**, W. R. B.; Dominion Museum, Wellington, N.Z.
 - A. **Omer-Cooper**, Prof. J., M.A., M.Sc.; Armstrong College, Newcastle-upon-Tyne.
- E. **Orr**, M. Y.; Royal Botanic Gardens, Edinburgh.
- E. **Osborn**, Prof. T. G. B.; Dept. of Botany, Sydney University, Sydney, N.S.W.
- E. **Osmaston**, A. E.; Principal and Professor of Forestry, Forest College, Dehra Dun, U.P., India.
- E. **Paltridge**, T. B.; Koonamore Vegetation Reserve, Koonamore, S. Australia.
- E. A. **Park**, Dr O.; Zoological Dept., University of Illinois, Urbana, Ill., U.S.A.
- E. **Peace**, T. R., M.A.; Imperial Forestry Institute, Oxford.
 - A. **Peacock**, Prof. A. D., D.Sc., F.R.S.E.; University College, Dundee.
- E. **Pearsall**, W. H., D.Sc.; Botany Dept., The University, Leeds.
- E. **Pearsall**, W. H.; Greengable, Matfield, Kent.
 - A. **Pentelow**, F. T. K.; Fisheries Research Station, Alresford, Hampshire.
 - A. **Percival**, E.; Canterbury College, Christchurch, New Zealand.
- E. A. **Perthshire Soc. of Nat. Science** (Secretary, John Ritchie); Perthshire Soc. of Nat. Science Museum, Perth, Scotland.
- E. **Petch**, C. P.; Sundial House, North Wootton, King's Lynn, Norfolk.
- E. **Phillips**, Prof. J. F. V., D.Sc.; University of Witwatersrand, Milner Park, Johannesburg, Transvaal.
 - A. **Pickles**, W.; 23, Beech Grove Avenue, Garforth, Leeds, Yorks.
- E. **Pilling**, M., Ph.D.; Croft House, Outlane, Huddersfield.
- A. **Pitt**, F.; The Albynes, Bridgenorth, Salop.
- E. **Pitt-Schenkel**, J.; Forest Dept., Lushoto, Tanganyika Territory.
- E. **Powell**, Miss Doris, M.Sc.; Aldersyde, Reigate, Surrey.

- E. A. **Praeger**, Dr R. Lloyd; Royal Irish Academy, 19, Dawson Street, Dublin.
- E. **Priestley**, Prof. J. H., B.Sc.; The University, Leeds.
- E. **Ramsbottom**, J., M.A., O.B.E.; Botanical Dept., British Museum (Nat. History), London. S.W. 7.
- A. **Ratcliffe**, F. N., B.A.; Nat. History Dept., Marischal College, Aberdeen.
- E. **Rayner**, Dr M. C.; Bedford College, University of London, Regent's Park, London, N.W. 1.
- E. **Rees**, T. Kenneth; University College, Singleton Road, Swansea, S. Wales.
- E. **Rees**, J., B.A., B.Sc.; University College, Cardiff.
- E. **Regel**, Prof. Constantin; The Botanical Garden, Kaunas (Kovno), Lithuania.
- A. **Reid**, D. M.; Science Schools, Harrow-on-the-Hill, Middlesex.
- E. A. **Renouf**, Prof. L. P. W.; University College, Cork, I.F.S.
- E. **Rice**, C. H., B.Sc.; 20, Dyson Road, Leytonstone.
- E. A. **Richards**, O. W.; 29 a, Edith Road, London, W. 14.
- E. **Richards**, P. W.; Trinity College, Cambridge.
- A. **Ritchie**, Prof. J., M.A., D.Sc.; Marischal College, Aberdeen.
- Ritson**, Miss K. E.; 86, Boundary Road, St John's Wood, London, N.W. 8 (*Associate Member*).
- A. **Ritson**, W.; 12, West Street, Warrington, Lanes.
- E. A. **Robbins**, Prof. C. R., M.C., M.A.; c/o Messrs Lloyds Bank, 6, Pall Mall, London, W. 1.
- A. **Roberts**, B. B.; Bishopsgarth, Woking, Surrey.
- A. **Roberts**, J. I.; Medical Research Lab., Box 141, Nairobi, Kenya Colony.
- E. **Rogers**, Miss M. H., Green Bank, Four Oaks, Warwicks.
- E. **Ross**, R.; Botany School, Cambridge.
- E. **Rübel**, Dr E.; Zürichbergstrasse 30, Zürich, Switzerland.
- A. **Rushton**, W., D.Sc.; Biological Dept., St Thomas's Hospital Medical School, Albert Embankment, London, S.E. 1.
- A. **Russell**, Dr E. S.; 8, Steele's Road, London, N.W. 3, *Vice-President*.
- E. **Russell-Wells**, Miss B., Ph.D.; Botany Dept., University College, London, W.C. 1.
- E. **Sager**, J. L., M.A.; University College, Exeter.
- E. A. **Salisbury**, Prof. E. J., F.R.S.; Willow Pool, Radlett, Herts.
- E. **Sandwith**, N. Y., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Saunders**, Miss E. R.; 10, Newnham Terrace, Cambridge.
- E. A. **Saunders**, J. T., M.A.; Christ's College, Cambridge.
- A. **Savage**, R. M.; 19, Derwent Avenue, London, N.W. 7.
- E. **Schröter**, Prof. C.; Bellerivestrasse 65, Zürich, Switzerland, *Hon. Life Member*.
- A. **Scourfield**, D. J., I.S.O., F.L.S.; 6, Chadwick Road, Leytonstone, London, E. 11.
- Selwood**, Miss G. F.; 49, Blenheim Road, Moseley, Birmingham (*Associate Member*).
- E. **Sernander**, Prof. R.; Vaxtbiologiska Institutionen, Upsala, Sweden.
- E. **Shantz**, Pres. H. L.; University of Arizona, Tucson, Arizona, U.S.A.
- E. A. **Shelford**, Prof. Victor E.; Vivarium Building, Wright and Healey Streets, Champaign, Ill., U.S.A.
- E. **Sherrin**, W. R.; South London Bot. Inst., 323, Norwood Road, Herne Hill, London, S.W. 24.
- E. **Shirk**, C. J., Ph.D.; Nebraska Wesleyan University, Lincoln, Nebraska, U.S.A.
- A. **Shorrock**, W. G.; Morland Hall, nr Penrith, Westmorland.
- E. **Singh**, Prof. B. N., D.Sc.; Institute of Agricultural Research, Benares Hindu University, Benares, India.
- E. **Skene**, Macgregor, D.Sc.; The University, Bristol.
- E. **von Spö**, Prof. Rudolf; Debrécen, Hungary.
- E. **Sperrin-Johnson**, Dr J. C.; Botany Dept., University College, Cork.

- E. **Sprague**, T. A., D.Sc.; Royal Botanic Gardens, Kew, Surrey.
- E. **Stamp**, Dr L. Dudley; London School of Economics, London, W.C. 2.
- E. **Stanchinsky**, Vladimir; University of Smolensk, Smolensk, U.S.S.R. (Russia).
- E. **Stapledon**, R. G., M.A.; University College, Aberystwyth.
 - A. **Stephenson**, Prof. T. A., D.Sc.; The University, Rondebosch, Cape Town, S. Africa.
- E. **Stevenson**, Miss E. H.; The Training College, The Close, Salisbury.
- E. A. **Steward**, F. C., Ph.D.; Dept. of Botany, Birkbeck College, Bream's Buildings, Fetter Lane, London, E.C. 4.
- E. **Stiles**, Prof. W., M.A., F.R.S.; The University, Birmingham.
 - A. **Storrow**, B., M.Sc.; Dove Marine Lab., Cullercoats, Northumberland.
- E. **Summerhayes**, V. S., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Swabey**, C.; Forest Department, Port of Spain, Trinidad, B.W.I.
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A STUDY OF THE NATURAL CONTROL OF RAGWORT (*SENECIO JACOBÆA* L.)

By EWEN CAMERON, B.Sc., F.R.E.S.

(Imperial Institute of Entomology.)

(With Plates XX, XXI and eleven Figures in the Text.)

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INTRODUCTION.

WITHIN the last ten or twelve years that branch of economic entomology which aims at the suppression of noxious weeds by the application of biological measures has come to occupy an increasingly prominent position in the field of Empire research. More especially is this true of the countries "down under"—New Zealand, Australia, and the islands of Fiji—where extensive studies and field operations on the problem of controlling various introduced weeds by the agency of phytophagous insects have been carried out.

Weeds may be defined economically as plants which are not only useless to man, but are also injurious to crops and stock reared by man. Wherever agriculture exists, weeds occur. They vary greatly in importance, but even when they are relatively innocuous in their native homes, they often become extremely injurious when introduced into new environments. In these new environments, freed from the restricting influences which held them in check in the homeland, they rapidly assume the proportions of pests, provided of course that restrictive influences equal in potency to those of the homeland are not present. It is to the weed pest, characteristic of these conditions, that biologists are attempting to apply the method of natural control.

The present paper comprises a short account of the New Zealand Weed Control Scheme, a summary of previous attempts to subjugate weeds by the biological method, a study of the ecology and natural control of ragwort (*Senecio jacobaea* L.), a weed accidentally introduced from Europe into several other parts of the world, a description of the methods used in dealing with the natural enemies of this plant, and a discussion of the possibilities of biological control in the particular species under consideration.

I. THE BIOLOGICAL CONTROL OF WEEDS IN NEW ZEALAND.

The attempt to control weeds in New Zealand by the biological method was initiated by Dr R. J. Tillyard, who, in 1927, with the help of grants from the Empire Marketing Board, the New Zealand Government, and the Cawthron Institute Trustees, established a laboratory for this purpose at the Cawthron Institute, Nelson, New Zealand. In Europe, the initial investigations were mainly carried out at the Rothamsted Experiment Station by entomologists working under the supervision of Dr A. D. Imms; later, in 1929, this work was transferred to the Parasite Laboratory of the Imperial Institute of Entomology at Farnham Royal, where Dr A. S. Watt and Mr E. H. Chater carried out an investigation on gorse, and the present writer on ragwort.

The noxious plants brought under this Weed Control Scheme consisted of the four major weeds: *Senecio jacobaea* L. (ragwort), *Ulex europaeus* L. (gorse), *Rubus fruticosus* (agg.) L. (blackberry), and *Acaena sanguisorbae* (piri-piri or bidi-bidi). Later *Pteridium aquilinum* L. (Kuhn) (bracken), *Digitalis purpurea* L.

(foxglove), *Hypericum perforatum* L. (St John's wort), *Rumex* spp. (dock), and *Urtica dioica* L. (nettle) were included. All these weeds, with the exception of piri-piri, are native to Britain. Work has been carried out at Farnham Royal on ragwort, gorse, blackberry, and, to a lesser degree, on bracken. The present position of the work is summarised as follows:

Ragwort. The control of this weed being the subject of the present investigation, all details come later.

Gorse. Since gorse is useful for sheep fodder and also for supplying nitrogen to the soil, only partial control is desired. For this purpose the weevil, *Apion ulicis* Först., is being used. The larvae of *Apion* develop in the gorse pods and destroy a considerable number of the seeds. Initial difficulties were experienced in the breeding of the weevils in New Zealand, but they have now been overcome and *Apion* has been established in the field, where it plays a definite part in the control of gorse. Other insects, such as the moth *Laspeyresia ulicetana* Haw., might prove useful means of control, but they have not yet been investigated. A report on this part of the work has been published by Mr E. H. Chater (1931).

Blackberry. This weed is a very difficult one to deal with because it belongs to the family Rosaceae, which includes a very large number of most important economic plants. Several insects studied, such as the moths, *Thyatira batis* and *Bembecia marginata*, the gall-forming Buprestid, *Agrilus ruficollis*, and the midges *Perrisia plicatrix* and *Lasioptera rubi*, were discarded because of their propensity for attacking important allied food plants. The Buprestid beetle, *Coraeus rubi* L., appeared to be the most effective of the natural enemies. The larvae of this species, which is widely distributed throughout Western, Central, and Southern Europe, though absent from the British Isles, feed on the roots of blackberry; but they also attack tea roses (*Rosa indica*) and raspberry. However, so obnoxious had the blackberry pest become, that the authorities decided to overlook the danger to roses and raspberries, and imported large numbers of the larvae of the beetle in rose stocks from the Antibes area in Southern France, via Farnham Royal. Further tests showed that the adult fed on raspberry, loganberry, rose and apple. It has not yet been liberated in New Zealand.

Other insects that might prove useful as a control occur in America, but it is now probable that the attempt to control blackberry by insects will be abandoned, owing to the great risks to economic plants from the introduced insects.

Piri-piri. The sawfly, *Antholcus varinervis*, whose larvae feed on the leaves in winter and spring, has been imported from Chile, but has not yet been liberated in New Zealand.

Bracken. The insect enemies of bracken have not yet received adequate study. The caterpillars of *Hepialus hectus* L. feed on the roots, and several species of Anthomyiidae occur on the plant; but the damage caused seems, in

general, to be insignificant, and the possibility of control by natural enemies remote.

St John's wort. The insect enemies of this weed are being investigated by the Australian entomologists. They can easily be introduced into New Zealand if they prove effective in Australia.

No work has been done on dock, nettle, or foxglove.

Thus far only preliminary work has been carried out on the New Zealand projects, and it is too early to give any definite opinion as to the final results of the researches.

II. SUMMARY OF WEED CONTROL THROUGHOUT THE WORLD.

The following table shows the extent of the chief work carried out, or being carried out, on the biological control of weeds throughout the world:

Country	Weed	Homeland of weed	Results	Chief insects concerned
Hawaii	<i>Lantana camara</i>	Mexico	Complete control in certain areas	<i>Agromyza lantanæ</i> Frogg., <i>Crociosema lantanæ</i> Busck., <i>Thecla bazochii</i> God., <i>T. echion</i> L.
Australia	<i>Opuntia inermis</i> <i>O. stricta</i> <i>O. monacantha</i> <i>O. tomentosa</i> <i>O. aurantiaca</i> <i>O. streptacantha</i> (Prickly pear)	America	Prospects of control very promising	<i>Cactoblastis cactorum</i> plus bacillary rot; <i>Dactylopius indicus</i> and three strains of <i>D. tomentosus</i> (cochineals); <i>Chelinidea tabulata</i> (bug); <i>Moncilema ulkei</i> (longicorn); <i>Tetranychus opuntiae</i> (red spider)
	<i>Hypericum perforatum</i> (St John's wort)	Europe	Preliminary	<i>Chrysomela varians</i> , <i>C. hyperici</i> , <i>C. brunsvicensis</i> , <i>Lathronympha hypericana</i>
	<i>Xanthium spinosum</i> <i>X. pungens</i> (Cockle burrs)	America	Preliminary	—
	Weeds awaiting investigation: <i>Lepidium Draba</i> , <i>Kentrophyllum lanatum</i> , <i>Inula graveolens</i> , <i>Centaurea calcitrapa</i> , <i>Echium plantagineum</i> , <i>Chondrilla juncea</i> . For ragwort and gorse see New Zealand			
New Zealand	<i>Rubus fruticosus</i> L. (Blackberry)	Europe	Attempt abandoned	<i>Coræbus rubi</i> L. (Buprestid)
	<i>Senecio jacobaea</i> L. (Ragwort)	Europe	Prospects of control promising	<i>Tyria jacobaeæ</i> L., <i>Pegohylemyia seneciella</i> Meade
	<i>Ulex europæus</i> (Gorse)	Europe	Prospects of control fairly promising	<i>Apion ulicis</i> Först.
	<i>Acaena sanguisorbæ</i> (Piri-piri)	Chile	Prospects of control fairly promising	<i>Antholcus varinervis</i>
	<i>Pteridium aquilinum</i> (Bracken)	Europe	Preliminary investigations. Possibility of control remote	<i>Hepialus hectus</i> L. and spp. of Anthomyiidae
	Weeds awaiting investigation: <i>Digitalis purpurea</i> , <i>Rumex</i> spp., <i>Urtica dioica</i> . For <i>Hypericum perforatum</i> see Australia			
Fiji	<i>Lantana</i>	America	Control hopeful	<i>Teleonemia lantanæ</i>
	<i>Clidemia hirta</i>	—	Control in certain areas	<i>Liothrips urichi</i>

III. PRINCIPLES OF WEED CONTROL BY INSECTS.

The amount of work which is being carried on by entomologists all over the world in an attempt to check the ravages of introduced insects is sufficient evidence of the widespread destruction caused to valuable crops by such pests. Since phytophagous insects cause so much harm to economic plants if accidentally introduced, it seems that the planned introduction of suitable insects may cause similar damage to non-economic or noxious plants. This is the hypothesis underlying attempts to obtain the biological control of weeds¹.

If we do not expect too much of the method, all will be well; but if, on the other hand, we hope to see a rapid and complete clearance of the weed following on insect introduction and liberation, we shall probably be disappointed. To prove this statement, let us look at the position of accidentally introduced insect pests. There are instances, such as that of the citrus industry of California, where almost complete destruction of the crops has been threatened by introduced insect pests. Such complete destruction or extinction, however, is a term employed by the cultivators with reference to the financial aspect of the problem. It does not mean that the numbers of the plant have been reduced to zero. Biologically there may be, and usually are, enough numbers left to carry on the crop, although owing to the control exercised by the insect pest, it is not able to increase and produce fruit to such an extent that its cultivation is profitable. Similarly, introduced insects are not likely to exterminate weeds. It is much harder to kill plants with phytophagous insects than it is to kill phytophagous insects with their entomophagous enemies. Furthermore, as will be shown later, plants, under certain conditions, react to insect attack. The control of plants by insects is therefore more difficult to obtain than control of insects by insects.

However, a study of the damage caused by insect pests and of the results obtained by experiments strongly suggest that the biological control of weeds, which so far has only been attempted where infested areas are so extensive that they cannot be treated by other methods, may, in certain circumstances, be possible, that under favourable conditions the increase and spread of the weed may be checked, and the infestation reduced to a level at which the infested land becomes of some economic value, even though complete destruction of the weed is not attained.

One of the first points which presents itself in an investigation of this kind is the possibility that the weed-controlling insect will migrate from its normal host, the weed, to a plant of economic value. How the insect is going to act in its new home it is impossible to say, because the new environment may affect both the insect and the plant: their relations may remain the same, may

¹ The two instances are not quite parallel because many economic plants are maintained in a man-made environment and survive only so long as man's control; many too have their constitution undermined by cultivation and breeding.

converge or diverge—one cannot tell. Certain safeguards, however, may be taken against the fulfilment of this possibility of change of host. These are: (1) the choice of an insect with a limited host range; (2) of an insect with a specialised mode of life, such as a root-borer, seed feeder, etc., when the weed is closely allied to economic plants (see Imms, 1928); and (3) the carrying out of exhaustive tests of the insects on economic plants, especially on those allied to the weed.

Host change has already occurred in agricultural practice. The Colorado beetle, *Leptinotarsa decemlineata* Say, is a good example. This insect, which originally fed on the sand burr, *Solanum rostratum*, on the eastern slopes of the Rocky Mountains, migrated to *Solanum tuberosum*, the cultivated potato, of which it became a serious and widespread pest. The beetle, before the progress of agriculture altered its environment, was confined to its native food plant, but when large areas of potatoes were planted in its vicinity it migrated to the easier and more abundant source of food supply.

The Nymphalid, *Pyrameis cardui* L., which feeds generally on *Carduus* and *Urtica*, is another instance. In Poland the transference of this species to *Lupinus angustifolium*, and in the U.S.A. to peppermint and soy beans, has been recorded.

Several experiments have been conducted to determine the possibility of such changes of host plants. Pictet (quoted by Imms, 1928) placed larvae of *Lasiocampa quercus* L., which feed on deciduous trees and bushes, on *Pinus*, and many died. The survivors bit into the extremities of the pine needles and carried through to the next generation. The larvae of this second generation became so adapted to the new host that when offered leaves of deciduous trees they either starved, or attacked them at the apices, hollowing them out in a way similar to that in which their predecessors attacked the needles of *Pinus*.

Experiments of this kind have also been made by Heslop Harrison and others. Harrison was able to effect transference of the gall-forming sawfly, *Pontania salicis*, from *Salix phylicifolia* to *S. andersonii* and *S. rubra*. Although a great deal of work has not been done on this subject, these experiments, carried out on insects with a limited host range, but general feeders on foliage and flowers and not specialised as root-borers, stem-borers, and internal seed-feeders, indicate the possibility of insects changing on to new hosts, when their environment is altered. On the other hand, several investigators, including workers on weed control, with their extensive system of starvation tests, have failed to induce phytophagous insects to adopt new hosts and transmit their acquired preference.

Generally speaking, we find that when most insects, hitherto more or less restricted in host range, attack a new host, the new food plant is closely allied to the old one, and belongs to the same family, if not to the same genus. Overcrowding of the insects and the destruction of the natural wild host are two of the causes which induce migrations to new hosts. Once established on

its new food plant, the continuity and abundance of the latter explain the ultimate outbreak of the pest.

Another point we must not forget is that by the rigid exclusion of their parasites from the new country, weed-controlling insects are given a great advantage, though sometimes this is partly offset by the attack of native parasites.

The main principles underlying the biological control of weeds may thus be summarised as follows:

(i) Since accidentally introduced insects often have an extremely destructive effect on plants of economic value, purposely introduced suitable species may exercise a similarly destructive effect on plants of no value—or weeds.

(ii) The insects selected for control purposes should preferably be effective against the weed in its home country, although it may happen that an insect which is comparatively harmless in one environment may be more virulent in another, and *vice versa*.

(iii) They must also be more or less specific, or have a restricted host range. If the weed in question is isolated systematically and physiologically from plants of economic value, the problem is greatly simplified; if closely allied, then more specialised insects (see Imms, 1928), such as root-borers, seed-feeders, etc., and not leaf-feeders, should be employed, because leaf-feeders seem, on the whole, to be less specific in their habits than root-borers, etc.

(iv) The possibility of a change of host plant must be eliminated by exhaustive tests of the insects on economic plants, especially on those allied to the weed.

(v) Parasites must, so far as possible, be eliminated before export. If the material has been exposed to the attack of parasites in the field before collection great care must be taken in the country receiving the insects to see that all parasites that make their appearance are destroyed.

The procedure involved in the study of the insect fauna of a noxious weed, with a view to its biological control, is as follows:

(i) The compilation of a list of all insects recorded from the plant.

(ii) Life-history studies of those most suitable as controlling agents.

(iii) Starvation tests of the selected insects on economic plants related to the weed to be controlled, and on other plants open to the risk of attack.

(iv) The discovery of suitable methods for large scale collecting, sorting, and shipping parasite-free material.

This procedure has been followed in the present investigation.

IV. RAGWORT (*SENECIO JACOBAEA* L.).

(1) DESCRIPTION OF THE WEED.

Ragwort (*Senecio jacobaea* L.) is a member of the large Dicotyledonous family Compositae. A native weed of Britain and an introduced species in New Zealand, it is considered injurious in both countries. Although classed as a noxious weed, the suppression of which is compulsory under the Corn Production (Repeal) Acts, 1921, it is not of major importance in this country, except in a few areas, and is more or less controlled, partly by natural, and partly by artificial means.

In Britain *Senecio jacobaea* is a common weed in all sorts of places, but chiefly on waste land and pastoral land of poor quality, on derelict agricultural land, roadsides, sand-dunes, and in certain areas on good farm pastures and meadows. On well-cultivated land it is absent; good cultivation and farming prevent its establishment. On the other hand, in New Zealand, ragwort has increased and spread so rapidly that it is now a very serious pest. It is kept under control in well-cultivated regions, but in New Zealand there are large areas of bush grasslands only partially cleared of logs and stumps, which, on account of the heavy cost, are not at present tilled; it is in these areas and in the dairy pastures, more especially, that ragwort is a nuisance, not only as an occupant of otherwise useful land, but as a poisonous plant responsible for heavy mortality in stock. "The ragwort menace", says a North Island newspaper, "has recently been causing concern among settlers of the Bay of Plenty, and in particular, the Te Puke, Whakatane, and Tauranga districts. So bad has ragwort become this autumn, that farmers have been losing large numbers of stock. The weed has taken possession of grazing land at Ngawaro and on No. 3 Road area, and has grown as tall as five and six feet. Already one farmer in the district has lost 47 head of stock since January. On one occasion, when returning with his cows for the evening milking, one farmer at Ngawaro missed seven heifers and upon investigation he found them dead. Five draught horses were also dead. Other farmers in the district have also had losses of stock."

The plant is described in Bentham and Hooker's *British Flora* as follows: "*S. Jacobaea*, Linn.—Rootstock short and thick without creeping roots. Stems two to four feet high, erect, scarcely branched except at the top. Leaves with ovate, obovate, or narrow segments, coarsely toothed or pinnatifid, the terminal ones large and confluent, the lower ones smaller and distinct, all glabrous or with a loose woolly down, especially on the under side. Flower heads rather large, of a bright yellow, in a handsome, compact, terminal corymb. Involucral bracts tipped with black, the outer ones few and very small. Florets of the ray from 12 to 15, linear-oblong and spreading, occasionally, but rarely, deficient. Achenes of the disc covered with short hairs, those of the ray glabrous."

(2) LIFE HISTORY.

The seed. The "seeds" of ragwort are, in reality, fruits, each hard fruit containing a single seed. Such a reproductive unit is called an achene. The achenes of *S. jacobaea*, which are slightly tapered at each end, more especially towards the proximal end, are 2 mm. in length, and at the middle are 0.6 mm. in breadth. The fruit coat is ridged with approximately eight ridges round the circumference. (No transverse ribs are present; those in the figure merely being a shading effect.) On each ridge is a number of small hairs, which are about 0.66 mm. long. Attached to the distal end of the seed is an ingenious wind-dispersal mechanism—the pappus. This device somewhat resembles a parachute in its action. It consists of about sixty fine hairs attached to the distal end of the pericarp, each hair being about 6 mm. in length, approximately three times as long as the seed. These filaments are provided with a fairly regular arrangement of minute spines, which point away from the seed, and are slightly longer than the breadth of the filaments to which they are attached. The basal part of each filament, for a short distance, is closely waved. This is probably connected with the release action which effects the removal of the seed from the capitulum. The working of the "parachute" depends on the relative humidity of the air, and on the velocity of the wind. With a high relative humidity the hairs come together and render the mechanism inoperative. As the amount of moisture in the atmosphere becomes less, the filaments separate and bend over to form a parachute arrangement round the seed. By means of certain mathematical calculations (Small, 1919), the most effective angle at which the hairs are bent, together with the minimum amount of wind necessary for dispersal, can be determined. Given the conditions of a low relative humidity, a wind above a certain minimum velocity, and comparative freedom from obstacles, there is no limit to the distance of dispersal of a pappose fruit. The pappus is either a modified calyx structure, or, more probably, a specially evolved mechanism.

In England the seeds ripen about the latter part of August, the time varying with the locality and with the season.

Germination. Tests made in the laboratory with seeds from Farnham Royal and Achterneed, Ross-shire, Northern Scotland, showed that 80 per cent. were viable. On damp filter paper kept at a temperature of 15° C., the seeds began to germinate on the fourth day. By the eighth day, the majority had germinated, and while one or two belated germinations occurred up to the twentieth day, after that germination ceased. In the field, germination may occur at two possible periods: at the end of August, the most usual time, or at the beginning of the growing season in spring, the seed lying dormant throughout the winter. In the first case the seedling attains a certain size, but ceases to develop during the colder months, resuming its activities in the spring.

Experiments to ascertain the relation of germination to the depth of the seed in the soil, show that the best results are obtained when the seeds are

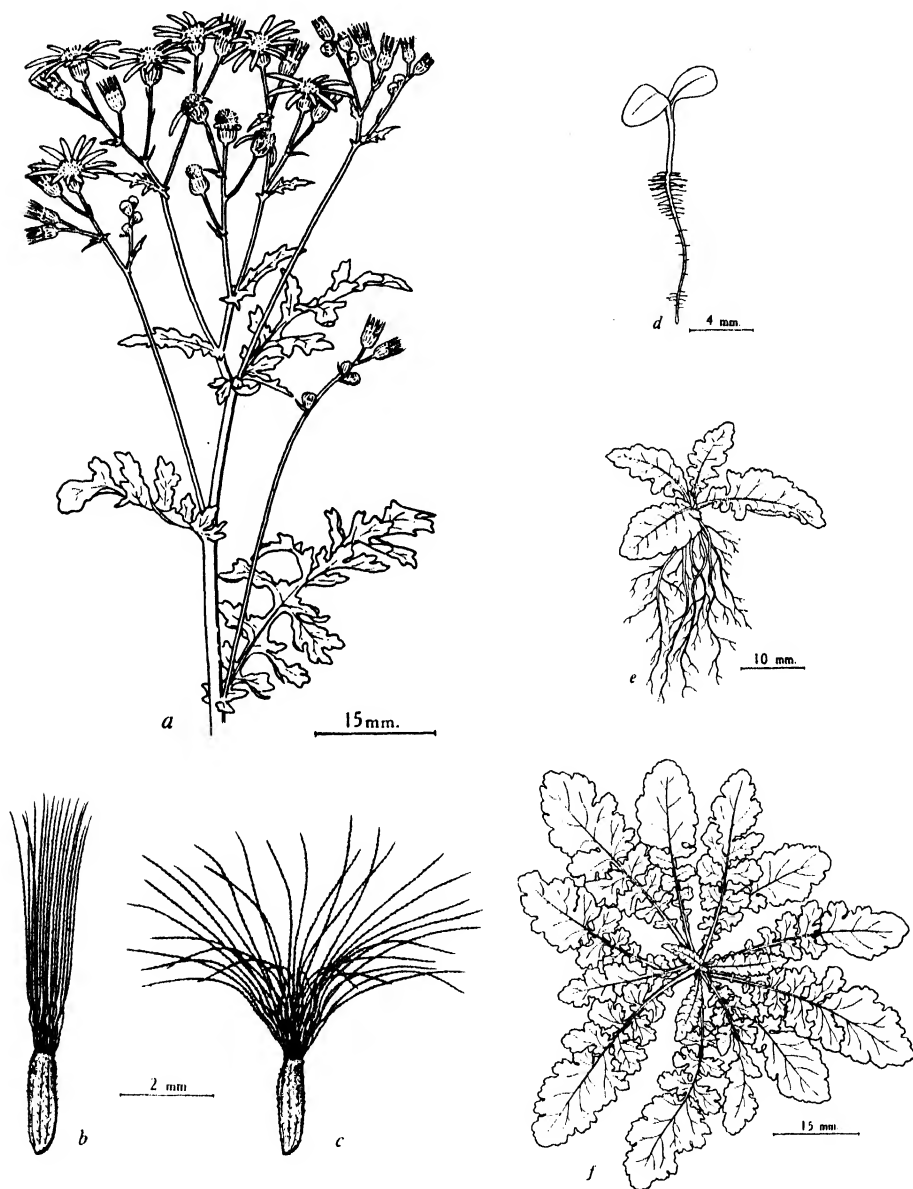


FIG. 1. Ragwort. *a*, cluster of capitula; *b*, seed with pappus closed; *c*, seed with pappus open; *d*, first stage seedling; *e*, second stage seedling; *f*, rosette.

just covered with soil. When they are buried at a depth of 1 cm. or more, no germination takes place.

The development of the seedling follows the usual course. At first two cotyledons appear, followed later by the plumule and leaves. The smooth margins of the latter soon take on the indented outline characteristic of mature ragwort. Growth continues until at the end of the first year the plant has assumed the form of a more or less flattened rosette. Just before the growing season in spring, the rosette measures 5–6 in. in diameter.

In the late spring the rosette (the plant is now in its second year) grows up rapidly to an average height of 2–4 ft., and often to 4 and 5, and sometimes even 6 ft., with one, two or more stems, which usually do not branch until near the top, where the numerous flower-heads form a compact terminal corymb. The flowers begin to open about mid-June and continue, from late secondary growth, till well on in the year, secondary flowers occurring even up to November. Pollination is effected by insect visitors, among which are the Hymenoptera *Apis mellifica*, *Bombus lapidarius*, *B. terrestris*, *B. hortorum*, *Sicus ferrugineus*, *Halictus* sp., and the Diptera *Eristalis tenax*, *Lucilia caesar*, *L. sericata*, *Calliphora erythrocephala*.

In *Senecio jacobaea*, as in other Compositae, we find an admirable adaptation for pollination. The crowding of the florets into capitula ensures that a single insect will pollinate a large number of flowers, and the earlier ripening of the male organs favours cross-pollination.

The seeds begin to set and ripen about mid-August, and are then distributed by wind. In order to ascertain the average number of seeds produced by ragwort, plants from different areas were collected and the seeds counted. It was found that the average number of seeds per capitulum was about seventy, produced from thirteen outer or ray florets, and fifty-seven inner or disc florets. Although the number of seeds per capitulum remained fairly constant from area to area, the number of capitula per plant varied tremendously, according to the size of the plant and the quality of the soil on which it grew. The figures from several areas follow:

Area	No. of capitula	Average no. of seeds	Total no. of seeds
1. Henley-on-Thames, Oxon	68	70	4,760
2. Dorney, Bucks	70	70	4,900
3. Farnham Royal, Bucks	167	70	11,690
4. Medmenham B, Bucks	191	70	13,370
5. Wentworth A, Surrey	680	70	47,600
6. Wentworth B, Surrey	910	70	63,700
7. Wentworth C, Surrey	1682	70	117,740
8. Wentworth D, Surrey	1720	70	120,400
9. Medmenham A, Bucks	2489	70	174,230

Interpreting these figures we should expect to find: plants with 5000 seeds growing either in very poor soil, or in slightly better soil where the plants are closely massed together; plants with 10,000–15,000 seeds, which is the commonest number, growing in medium to poor quality soil where the numbers of ragwort are not very high; and plants of 40,000 seeds and over growing in good soil, such as good agricultural land left derelict for building purposes, etc.

Plants producing 150,000–200,000 seeds do not often occur. The Medmenham A area figure was obtained from plants pruned the previous year, which made them three-year-old plants developing secondarily, with an unusually large production of capitula.

Ragwort is commonly known as a biennial, but I find that the length of its life period varies considerably. Generally speaking, a strong, well-grown plant, which has produced abundant seeds and is not disturbed, completes its life cycle in two years and is thus a biennial. On the other hand, a plant which has been interfered with in certain ways may become a perennial, the length of the life cycle then depending upon the action of the environmental factors affecting development. The causes most commonly producing this effect are the cutting down of the plant during agricultural operations or as a control measure, and the destruction of the flowers, leaves, and parts of the stems by phytophagous insects. Plants injured in this way, but still possessing a certain amount of reserve food, reproduce themselves by means of late secondary shoots and flowers. This secondary flower growth may result in the production of new seeds, equal to as much as 35 per cent. of the number that would have been produced by the uninjured plant, though the seed production of such plants is usually less. Where secondary flower production is not so extensive a number of basal shoots appear in the late autumn and in the spring of the following year. These shoots carry on the plant for another year, the new plants often being much larger and having more stems than the old. If this new plant of secondary origin is again cut down by man, or grazed by animals, a similar reaction takes place, and so on, till the weed finally loses all its vitality and dies. We thus have, in addition to the ordinary biennial ragwort, a very large number of individuals becoming what may be called *induced perennials*.

The spread and success of ragwort is thus principally due to: (1) the wind-dispersal mechanism—the pappus; (2) the effective multiple pollination method; and (3) the production of plants and flowers secondarily.

(3) HISTORY OF RAGWORT IN NEW ZEALAND.

Ragwort was introduced into New Zealand prior to 1874, in which year Thomson records it from Dunedin. Its increase was rapid, and it is now found in almost every provincial district in the Dominion. It had become so troublesome that it was declared a noxious weed in the first schedule of the Act of 1908.

Other introduced species of *Senecio* exist in New Zealand: *S. vulgaris* L., *S. sylvaticus* L., *S. erucifolius* L., *S. aquaticus* Huds. and *S. mikanioides* Otto.; but none of these is of great economic importance.

(4) ECONOMIC STATUS AND IMPORTANCE.

Senecio is the largest of the Compositae genera, being spread all over the globe, although the majority of the species occupy only small areas. Among flowering plants the Compositae, with about 900 genera and over 13,000

species, are one of the largest families, forming about one-tenth of the whole number of Angiosperms.

(i) *Economic allies.* Curiously enough, although important weeds are common among the family Compositae, food plants of economic importance are not. Those which have some economic value are merely a few minor vegetables, several plants of ornamental value, and some with medicinal properties. The food plants include lettuce (*Lactuca*), artichoke (*Cynara*), Jerusalem artichoke (*Helianthus*), chicory (*Cichorium*), etc. Amongst the ornamental plants are golden rod (*Solidago*), Michaelmas daisy (*Aster*), everlasting (*Helichrysum*), sunflower (*Helianthus*), *Dahlia*, *Chrysanthemum*, *Tanacetum*, *Cineraria*, *Calendula*, *Centaurea*, and *Echinops*. Those of medicinal value are chamomile (*Anthemis*), wormwood (*Artemisia*), coltsfoot (*Tussilago*), and *Arnica*. Within recent years *Chrysanthemum cinerariaefolium* Trev. has risen to prominence. From its dried flowers the insecticide pyrethrum is manufactured. Two other species, *C. coccineum* Willd. and *C. marschali* Ascher, also possess insecticidal properties, but *cinerariaefolium* is by far the most important. It is a native of the Mediterranean and is cultivated in Japan, which supplies 70 per cent. of the world's requirements of pyrethrum. It is also grown in France, Switzerland, and North Africa for home consumption. An attempt is being made to produce it commercially in England.

(ii) *Noxious properties.* Ragwort is injurious to farming interests in two ways. Firstly, it has taken possession of large areas of land, suitable for grazing, and, secondarily, it is poisonous to stock. *Winton Disease*, so-called from the area in Southland where it first made its appearance, is the result of eating ragwort in quantity and causes a heavy mortality in horses, and also affects cattle and sheep. A similar disease, attributable to the same species of *Senecio*, occurs amongst cattle in Pictou, Nova Scotia, where it is known as *Pictou Disease*. In Norway, *Sirasyke* is probably the same disease. All three are characterised by the same symptoms described later in this paper.

In Britain this disease is supposed to be comparatively rare. Quite recently (November 1929) in Ireland, a number of veterinary specialists presented their report to the Veterinary Medical Association of Ireland on liver cirrhosis in horses and ragwort poisoning in cattle, both affections following on the ingestion of *Senecio jacobaea* L. It appears from their researches that this type of poisoning is more common than is generally supposed. The cases noted were confined to the poorer types of pasture, where weeds, including ragwort in abundance, were present. In England several deaths have occurred among cattle as a result of eating large quantities of ragwort in dried hay. Generally speaking, however, stock, with the exception of sheep, do not eat the plant unless compelled to do so; for example, when pasture has dried up and ragwort still remains green and juicy. It is chiefly in such situations that deaths from ragwort poisoning are common in New Zealand and South Africa. In the latter country, however, two allied species, *S. retrorsus* and *S. burchelli*, are

to blame for the disease, known as *Molteno Disease*. Sheep must be placed in a separate category in regard to this malady. They are tolerant to the weed, and even eat it with avidity, so much so indeed that they have been used as a means of getting rid of the pest, often with a great measure of success. The cumulative action of the poison, however, after a long period of grazing on ragwort-infested pastures, is fatal.

(iii) *Symptoms of ragwort poisoning.* These appear after one to three months' continued grazing on the plant, and even if, at the end of this period, cattle are removed from the infested pasture, while still apparently healthy, symptoms may subsequently develop, leading to fatal results. In the early stages the animals appear hidebound, later they have a staggering gait and become partially blind. They may get very excitable and charge anyone who approaches them. In some, diarrhoea may be present, but normally constipation is very marked. At death, in the earlier stages of the poisoning, the principal lesion is an inflammation of the bowel. In acute cases the liver is firmer than normal, and yellow in colour. In chronic cases the liver is hard, owing to increase in fibrous tissue, a condition described as hepatic cirrhosis, and in those so affected the abdominal cavity contains fluid. The lungs are congested.

V. THE ECOLOGY AND NATURAL CONTROL OF RAGWORT.

Any weed-control investigation which does not take into account the influence of environmental factors (other than insects) on the weed, is far from complete. In this section an attempt is made to identify and evaluate the importance of the ecological factors determining the distribution, vigour and numbers of ragwort.

Ragwort is distributed throughout Great Britain, chiefly on light sandy soils, waste places, roadsides, sand-dune areas, derelict agricultural land and overgrazed pastures. To the ecologist this distribution indicates ragwort to be a plant which requires for its establishment a disturbed soil surface, where the plant community has been broken. Of the four groups of ecological factors affecting plants (climatic, physiographic, edaphic and biotic), the biotic is by far the most important in setting limits to the distribution of ragwort. The edaphic and climatic are important in so far as they affect the vigour of the weed and of its competitors, while the physiographic, for the purpose of this investigation, is relatively unimportant.

(1) CLIMATIC CONTROLLING FACTORS.

In Britain, ragwort is fairly abundant in favourable habitats, from the south coast of England up to Sutherlandshire in Scotland, and probably to the northern seaboard. It grows in areas of low and of high rainfall. Plenty of sunlight is necessary, as ragwort is normally a plant of open situations, and the seedling dies if deprived of the necessary light intensity by taller growing plants.

It must not be forgotten that the four groups of ecological factors interact. Rainfall influences and alters the edaphic factor, which in its turn reacts on the biotic, while the latter is also directly affected by climate. Bearing all this in mind, we can say that the climate of Britain is well within the range necessary to ragwort, although variation in the weather affects its vigour and recuperative powers.

(2) EDAPHIC CONTROLLING FACTORS.

Ragwort is essentially a plant of well-drained and even dry soils. It grows on the shallow, highly calcareous soils derived from chalk (*vide* Watt), on sand-dunes, on chalky sands, on derelict arable land, and neglected and overgrazed enclosed pastures. Some of these soils contain much calcium carbonate and are alkaline, and we may assume the rest to contain some free calcium carbonate and to have a low acidity. Ragwort, on the other hand, is absent from the very acid carbonate-free sandy soils of parts of Breckland. It would thus appear that ragwort grows more commonly on soils of low acidity. Yet it is found on certain somewhat anomalous soils of the Chiltern plateau, where the soil is a loam, is fertile, highly acid ($pH\ 5.2-4.7$), contains no free calcium carbonate, and has a low exchangeable calcium content, and a low basicity. The one factor common to all the habitats is a well-drained soil.

Within the soil range of ragwort, its frequency bears no relation to soil type, but is closely correlated with the area of bare soil offered for seed germination and seedling establishment. In naturally open plant communities, like the earlier stages of vegetation on sand-dunes, ragwort is frequent; its high frequency in other normally closed plant communities is due to the breaking of the vegetation cover by the direct and indirect interference of man; in short to the biotic factor.

(3) BIOTIC CONTROLLING FACTORS.

The influence of biotic factors on ragwort control and distribution is of considerable importance. Two groups of such factors, one botanical and the other zoological, may be recognised.

(α) Botanical.

Field observations. Most of the plants which have an important influence on ragwort belong to the family Gramineae. In Britain ragwort is absent from well-managed pastures on fairly good soil; long grass or close continuous turf effectively prevent its establishment, even although seed may be abundant. This was clearly demonstrated in the summer of 1930 at Hambledon, Bucks., and Buckenham, Norfolk. At Hambledon a field was divided into three natural areas of approximately ten acres each. Area 1 had a long thick sward of the grass, *Brachypodium pinnatum* L. (false brome), and was devoid of ragwort. Area 2 was a much overgrazed pasture, consisting of the following grasses:

Holcus mollis, *H. lanatus*, *Anthoxanthum odoratum*, *Dactylis glomerata*, *Phleum pratense*, *Lolium perenne*, and *Poa trivialis*. This area bore 4000 ragwort plants

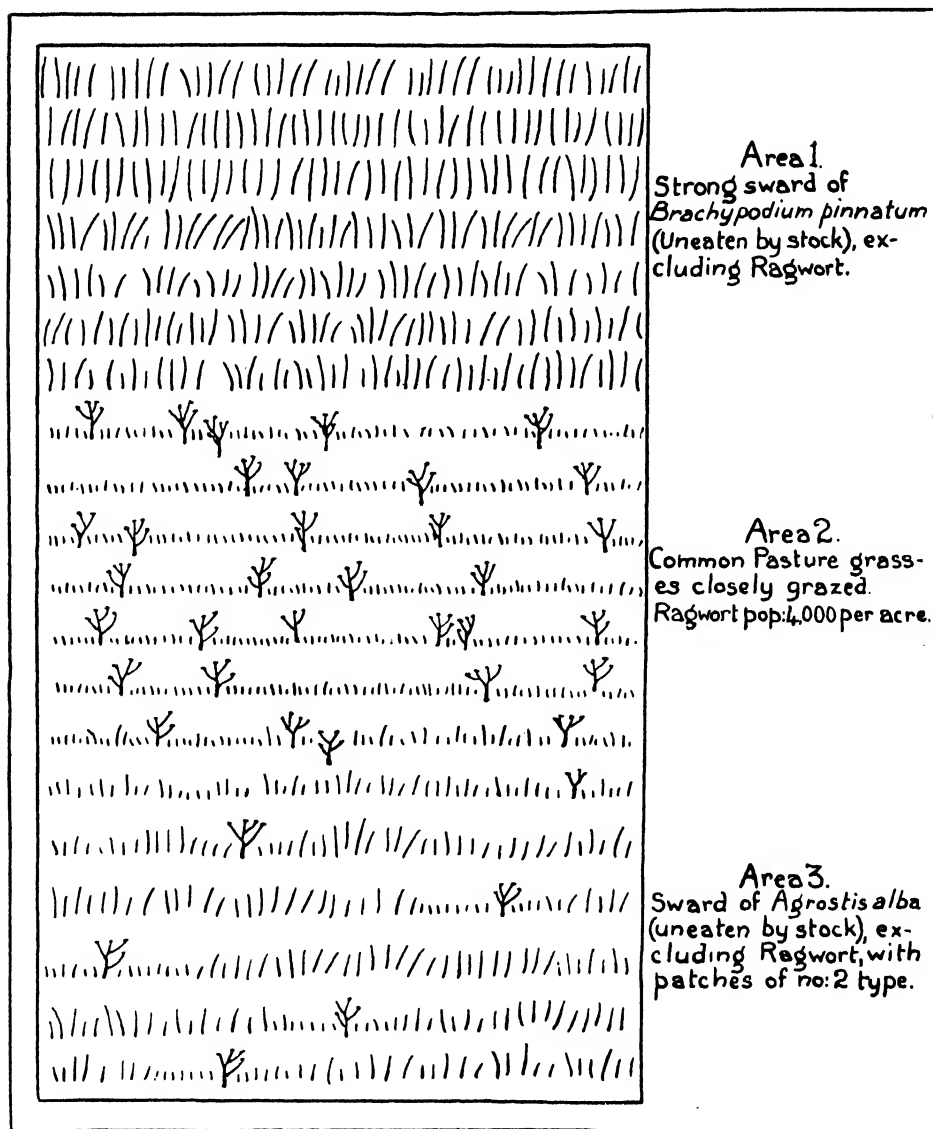


FIG. 2. Illustrating the effect of close grazing on the establishment of ragwort, and of thick sward on the exclusion of the weed. (Area of field, 30 acres.)

per acre. Area 3 was not so overgrazed and bore large quantities of *Agrostis alba*, which was not eaten by the stock. Where it grew thickly it practically excluded ragwort. In certain places the soil was exposed and herbage of the number 2 type with ragwort occurred. The two grasses, *Brachypodium pinnatum*

and *Agrostis alba*, which were so effective in excluding ragwort, were probably not greatly relished by the stock. Nevertheless, the effect produced by them indicates the importance of rank herbage and the necessity of avoiding over-grazing in ragwort control.

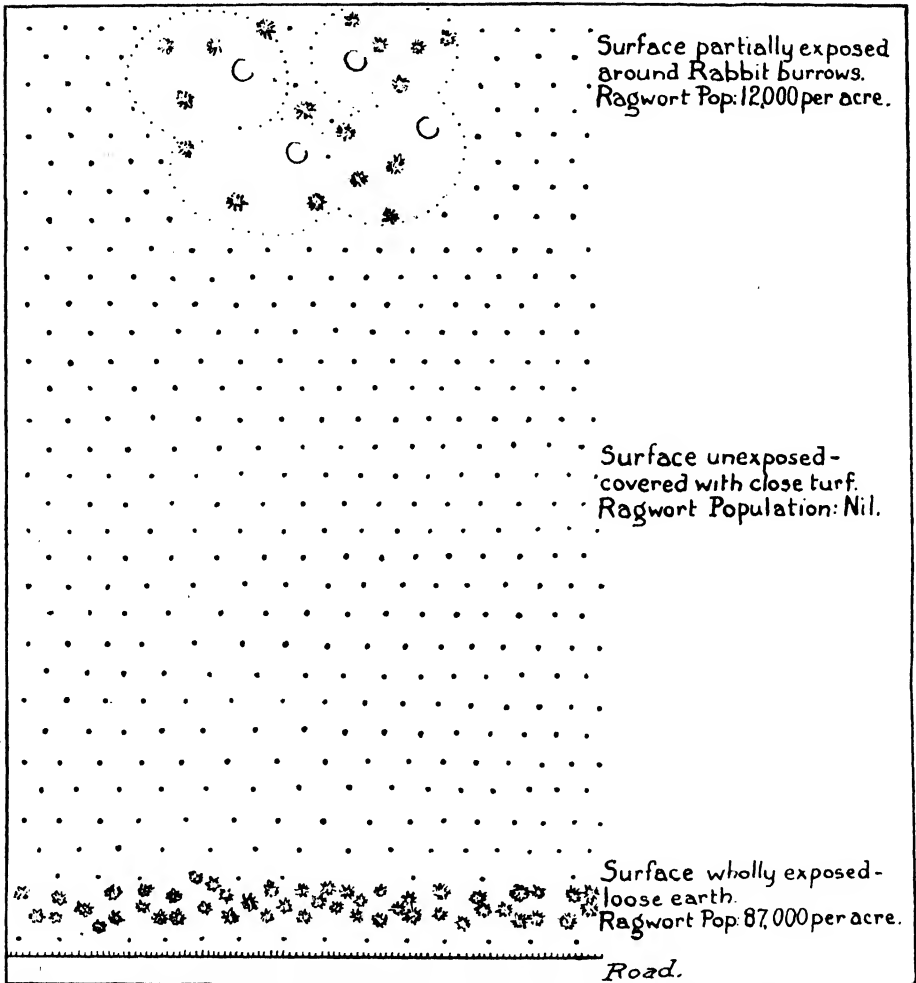


FIG. 3. Illustrating the effect of exposed soil surface on the establishment of ragwort seedlings.

To this positive evidence of the value of a good sward, we may add evidence, which although negative is corroborative. If strong grass competition excludes ragwort from the composition of the pasture, the entire absence of competition should greatly encourage the establishment of the weed. The following observations from Buckenham, Norfolk, endorse this statement: An area by the roadside, 150 yards long and about 2 ft. wide, consisting of loose soil thrown up by the roadmen, had a population of two

ragwort rosettes per square foot, or 87,000 per acre. Immediately within this strip *the land was covered with a close continuous turf in which there was no ragwort*. Still further in, about 90 yards from the road, this turf was riddled with rabbit burrows. An area measuring 12 ft. by 7 ft. (84 sq. ft.) surrounding four large burrows was examined and the following data obtained: mature ragwort plants on area 22; rosettes 21; mature plants per acre 12,000. In this area we have thus three zones; one where grass competition is absent and the ragwort population is 87,000 per acre; another where it is greatly reduced by the burrowing of rabbits and the ragwort population is 12,000 per acre; and a third where it is so severe that ragwort is entirely excluded.

Other similar areas were observed in Norfolk. It is evident that the chief cause of ragwort abundance in that county is the comparative ease with which the plant can become established in the open plant communities of derelict arable land. The activities of rabbits tend to maintain the open community and provide suitable *nidi* for the establishment of the ragwort.

From these observations in the field, two main points emerge: first, ragwort does not become established where the plant community is unbroken—such as when the soil surface is covered with rank herbage or with a short and closely grazed but continuous turf; and secondly, where the plant community is broken and the soil surface exposed either by the action of rabbits in burrowing or by that of farm animals in overgrazing, ragwort can become established.

Experiments. So much for field observations on the influence of plant communities on ragwort. The following confirmatory experiments were carried out in the Laboratory garden to determine the effect of rank grass, rank grass cut down, short but continuous turf, and of bare surface on ragwort establishment. Six plots, each 1 ft. square, were prepared as follows: (1) long grass; (2) long grass cut short; (3) short but continuous turf; (4) hard compacted soil; (5) ordinary tilth, seeds uncovered; (6) ordinary tilth, seeds covered. The difference between (2) and (3) may be explained as follows: in (2) the grass consists of short single stems with consequent tiny areas of exposed soil in between, somewhat similar to the effect obtained in overgrazing; whereas in (3) tillering or multiplication of stems has taken place, and instead of single stems there are small clusters or tufts of stems, forming a continuous mat which completely covers the soil surface—this is what we find in a well-managed pasture.

On each of these six plots, one hundred ragwort seeds were evenly distributed (viability of the seeds 80 per cent.). On examination one to two months later, the following numbers of seedlings were found: plot 1, no seedlings; plot 2, two seedlings; plot 3, no seedlings; plot 4, twenty seedlings; plot 5, fifty-three seedlings; plot 6, fifty-five seedlings.

An analysis of these figures shows that long grass in plot 1 and short but continuous turf in plot 3 completely excluded ragwort. What the exact causes of non-establishment were, whether the seeds could not germinate in plot 1 through the absence of light, or in plot 3 through insufficient moisture, or

whether in the event of germination the low light intensity suppressed the seedling, was not determined. However, the main point is that the observations made in the field—that long grass and short continuous turf effectively exclude ragwort—are confirmed by the results obtained from plots 1 and 3. In plot 2 a few seedlings became established in the exposed soil between the single stems—this supports the field observations on the effect of overgrazing on the establishment of ragwort; in plot 4, where the ground was hard, the seedlings were younger and of varying sizes and ages. Establishment appeared to have taken place where the ground was penetrated and softened at points by rain and worm casts; the physical condition of the soil may have increased the number of seedlings in this plot. In plots 5 and 6 a large number of seedlings were obtained, and it did not seem to make any difference whether the seeds were covered or not.

From this experiment we may infer that if a large amount of seed (about 100 per square foot) settled on four different types of field, it is possible for seedlings to arise in the following proportions:

On long grass	No ragwort seedlings per acre
On short but continuous turf	No ragwort seedlings per acre
On overgrazed pasture	86,120 ragwort seedlings per acre
On hard exposed soil	871,200 ragwort seedlings per acre
On open soil	2,308,680 ragwort seedlings per acre

These figures are endorsed by field observations. Of course, a uniform covering of 100 seeds per square foot is never obtained, and, if it were, a very large number of seedlings arising from such a dense covering would succumb in the intraspecific competition. The results of the experiment agree with the evidence from the natural areas at Hambledon and Buckenham.

It is evident then from these experiments and observations, that when considering ways and means for the natural control of ragwort, the condition of the pasture is of the greatest importance and must not be neglected. Good farming, good range management, and ragwort abundance are incompatible. Many of the dairy farms of New Zealand, which are heavily infested with the weed, exhibit evidences of extensive overgrazing, and this state of affairs must be remedied before ragwort can be brought appreciably under control.

(β) Zoological.

The chief zoological factors influencing ragwort in this country are four in number: man, sheep, rabbits, and insects.

(a) *Man, rabbits and sheep.*

The influence of *man* may be direct, as in measures explicitly directed to the extirpation of the weed, or indirect, as in the conduct of farming operations not specifically directed against ragwort, but resulting in conditions such as those described in the preceding section, which are, in fact, unfavourable to it.

The effect exerted by *rabbits* in burrowing has already been mentioned. When dealing with the effect of exposed soil on the establishment of ragwort, it was pointed out that the areas immediately surrounding the rabbit burrows in the light, sandy soil of Norfolk, are suitable seed beds for the weed. As well as this open burrowing on large stretches of the desolate East Anglian heaths and other regions, an additional effect favourable to ragwort establishment is produced by their close-grazing activities. A large field at Medmenham, Bucks, is a case in point. This field was surrounded by a wood, from which large numbers of rabbits emerged and closely cropped the sward of the fringe and for some distance inwards. Bare patches were exposed and ragwort from the neighbouring badly infested waste lands colonised the area to the extent of 580 plants per acre. (Pl. XX.)

The action of rabbits is thus, in general, distinctly favourable to the increase of ragwort. They do eat the plant, but only sparingly, and not enough to check it.

Sheep, on the other hand, are effective controlling agencies. They are very fond of ragwort, especially in the rosette stage, and are relatively little affected by its toxic principles.

(b) *The insects recorded from ragwort.*

The three biotic factors affecting ragwort that have been mentioned in the preceding paragraphs are, of course, already present in New Zealand. But the insect enemies of the plant in Europe were not introduced with it into its new home, and are thus of particular interest from the economic standpoint.

A number of insects from each of the following five orders: Lepidoptera, Diptera, Coleoptera, Hemiptera, and Thysanoptera, have been recorded from ragwort. (The figures refer to the month of the year.)

(i) LEPIDOPTERA.

Arctiidae.

(1) *Tyria jacobaeae* L.: moth 5, 6; larva 7, 8. Larvae attack flower-heads, leaves and stem. Britain north to Caledonian Canal, Europe to West Central Asia. Other host: *Senecio vulgaris*.

(2) *Arctia villica* L.: moth 6; larva 8-5; larvae attack leaves. England, Roxburgh, local, Europe to Turkestan. Other hosts: *Myosotis*, *Plantago*, *Rumex*, etc.

(3) *Arctia fuliginosa* Bd.: record.

Caradrinidae.

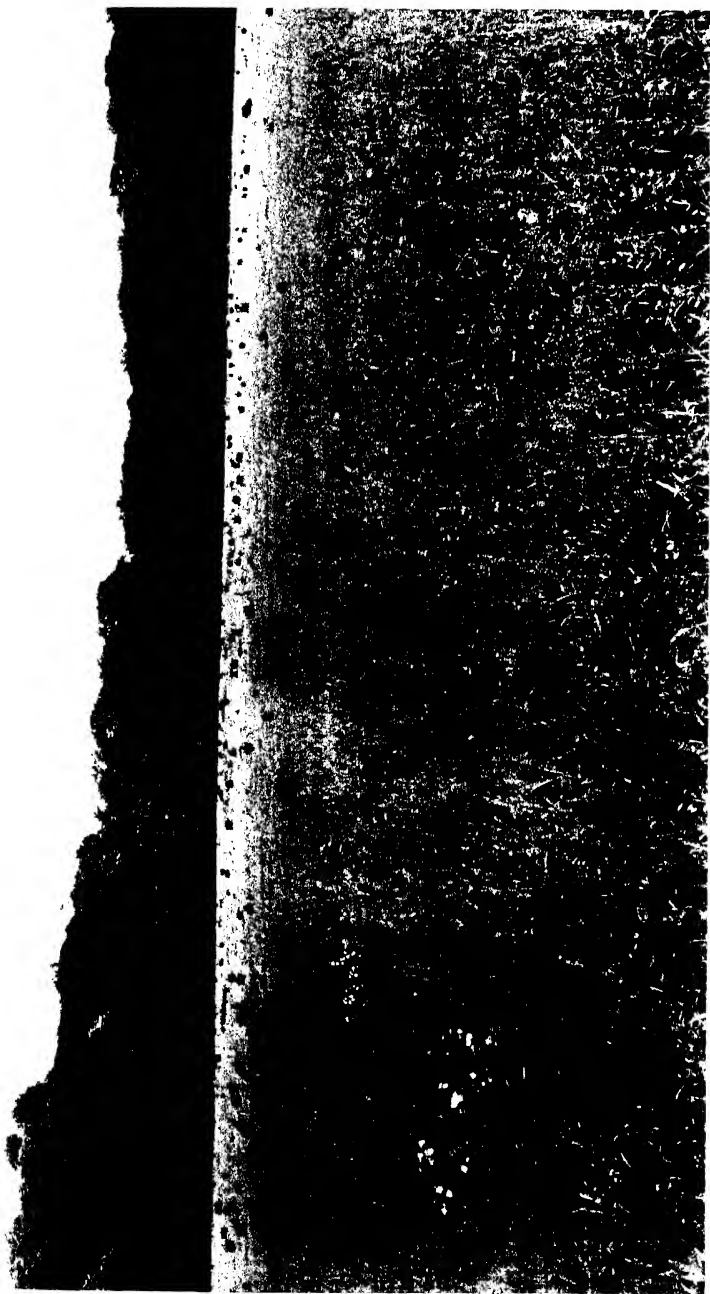
(4) *Hadena meticulosa* L.: moth 5, 6, 9, 10; larva 7, 8, 10-3. Britain to Shetlands, Ireland, common, Europe to Syria, Northern Africa. Other hosts: *Rumex*, *Viola*, etc.

(5) *Aporophylla (Epunda) luteolenta* Borkh.: moth 9; larva 10-4. Britain to Orkneys, Ireland, local, Europe. Other hosts: *Myosotis*, *Lithospermum*, *Achillea*, etc.

(6) *Polia lichenea* Hubn.: moth 8, 9; larva 11-5. Western England to Lancashire, Kent, Sussex, Yorkshire, Eastern Ireland, local. Other hosts: *Scabiosa*, *Rumex*, etc.

(7) *Agrotis (Pachnobia) simulans (pyrophila)*: record.

(8) *Ochria (Gortyna) ochracea* Hubn. (*flavago* Esp.): moth 8, 9; larva 5-8. In stems. Britain to Caledonian Canal, Ireland, rather local, Central Europe to Western Siberia. Other hosts: *Carduus*, *Arctium*, *Verbascum*, etc.



Phot. 1. Showing the effect of rabbits on Ragwort establishment. In the background a strong Ragwort colony has become established as a result of lowered grass competition, following on the close grazing action of numerous rabbits. The strong sward in the foreground, untouched by rabbits, has excluded the weed.

Plusiidae.

(9) *Plusia iota* L.: moth 6, 7; larva 8-5. Britain to Orkneys, Ireland, common, Northern and Central Europe to Western Turkestan. Other hosts: *Lamium*, *Urtica*, etc.

Hydriomenidae.

(10) *Eupithecia absinthiata* Clerck.: moth 6, 7; larva 8-10. On flowers. Britain to Ross-shire, Ireland, common. Northern and Central Europe to Eastern Siberia. Other hosts: *Artemisia*, *Achillea*, etc.

(11) *Eupithecia pimpinellata* Hubn. (*denotata* Guen.): moth 4, 5, 8; larva 6, 9, 10. England to Yorkshire, Eastern Ireland, Northern and Central Europe to Western Siberia. Other hosts: *Pimpinella*, *Achillea*, etc.

(12) *Eupithecia vulgata* Haw.: moth 5, 6; larva 7. Britain to Hebrides, Ireland, very common, Northern and Central Europe to Eastern Siberia. Other hosts: *Rubus*, etc.

(13) *Eupithecia oblongata* Thunb. (*centaureata* Fabr.): moth 5, 6, 8; larva 7, 9. Britain to Caledonian Canal, Western Ireland, common, Central and Southern Europe to Western Turkestan. On flowers and seeds of many Umbelliferae and Compositae.

(14) *Eupithecia castigata* Hubn. (*jasioneata* Crewe): moth 5, 6; larva 8, 9. Britain to Hebrides, Ireland, common, Europe to Eastern Siberia. Other hosts: *Scabiosa*, *Lychnis*, *Ononis*, *Epilobium*, etc.

(15) *Eupithecia virgaureata* Doubl. (*pimpinellata* Guen.): moth 5, 6; larva 8, 9. On flowers. England to Yorkshire, Ireland, local, Northern and Central Europe to Eastern Siberia. Other hosts: *Solidago*, etc.

(16) *Eupithecia expallidata* Doubl.: moth 7, 8; larva 9. On flowers. Southern and Western England to Lancashire, Aberdeen, Ireland, local. Central Europe. Other host: *Solidago virgaurea*.

(17) *Eupithecia (minutata* Guen.) *goossensiata* Mab.: moth 6, 7; larva 8-10. Britain to Orkneys, Ireland, common, Northern and Central Europe. Other hosts: *Erica*, *Calluna*, *Scabiosa*. Phycitidae.

(18) *Homeosoma cretaceella* Ross. (*senecionis* Vaughan): moth 5, 7; larva 6, 8, 9. In flower heads and stems. Southern England to Gloucester and Norfolk, on coasts, local, Holland, Germany, Siberia.

(19) *Homeosoma nimbella* Zell. (*saxicola* Vaughan): moth 6, 8; larva 7, 9. On flowers. Britain to Kirkeudbright, Eastern Ireland, on coasts, local, Europe to Palestine. Other hosts: *Anthemis*, *Jasione*, etc.

(20) *Homeosoma nebulella* Hubn.: moth 7, 8; larva 8, 9. On flowers. England to Yorkshire, rather common, Europe to Turkestan. Other hosts: *Carduus*, etc.

Pyraustidae.

(21) *Pyrausta alpinalis* Schiff.: moth 7, 8; larva 6. Amongst spun leaves. Clyde to Ross-shire, Northern Ireland (Antrim), mountains of Central Europe and Central Asia.

Phaloniadae.

(22) *Phalonia atricapitana* Steph.: moth 5, 6, 8; larva 7, 9-4. On flowers and stems. England, Roxburgh, Ireland, local, Central Europe to Siberia.

(23) *Phalonia dubitana* Hubn.: moth 6, 8; larva 7, 9. In seeds. Britain to Clyde, Northern Ireland, local, Northern and Central Europe to Siberia. Other hosts: *Crepis*, *Solidago*, etc.

(24) *Euxanthia aeneana* Hubn.: moth 6; larva 9-4. In stems and roots. Kent, Sussex, Surrey, Middlesex, Essex, local, West Central Europe. Other host: *Senecio paludosus*.

Eucosmidae.

(25) *Eucosma nigromaculana* Haw.: moth 6, 7; larva 9. In seeds. Britain to Clyde, Ireland, local, Central Europe.

(26) *Eucosma trigeminana* Steph.: moth 6, 7; larva 9-12. In roots. Britain to Sutherland, Eastern and Southern Ireland, rather local, Central Europe.

Coleophoridae.

(27) *Coleophora tricolor* Wals.: moth 7, 8. Sussex, Norfolk, local. Other hosts: *Triticum*, etc.

Records of Lepidoptera mostly from Meyrick, *British Lepidoptera*.

(ii) DIPTERA.

Cecidomyiidae.

(28) *Stictodiplosis jacobaeae* H. Loew. Attacks flowers and seeds, causing capitula to be strongly swollen and tinted red at base. Larvae gregarious. Records from all English counties except Cumberland. Recorded from *S. erucifolius* once in Co. Durham.

(29) *Cecidomyia* sp.: on ragwort and *S. aquaticus*. Several records from Northumberland and Durham.

Agromyzidae.

(30) *Agromyza aeneiventris* Flin.: larvae bore in stems.

(31) *Phytomyza albiceps* Meig.: larvae mine leaves. In leaves from June onwards. Common in Europe and America. Other hosts: *Chrysanthemum*, *Aconitum*, etc.

(32) *Phytomyza geniculata* Macq.: as *albiceps*. Europe.

Trypetidae.

(33) *Sphenella marginata* Flin.: larvae attack capitulum, causing feeble swelling at base. Solitary.

(34) *Ensina sonchi* L.: single male bred from flower heads by Richards.

Anthomyiidae.

(35) *Pegohylemyia jacobaeae* Hardy: adults emerge towards end of June. Larvae in capitula July–August.

(36) *Pegohylemyia seneciella* Meade: as *jacobaeae*.

(iii) COLEOPTERA.

Phytophaga: Halticidae.

(37) *Longitarsus dorsalis* F.: on *Senecio jacobaea* and *S. vulgaris*. Locally common in Isle of Wight, Ventnor, etc., London district, local and not common. Adult hibernates. Comes out about May; eggs, larvae and pupae follow between then and October, when a new generation emerges to hibernate as adults.

(38) *Longitarsus picipes* Steph.: on *Senecio jacobaea*. Very local but common where it occurs. Darenth Wood, Chatham, Northumberland district, etc. Life history as *dorsalis*.

(39) *Longitarsus jacobaeae* Wat.: on *Senecio jacobaea*. Common and generally distributed throughout the greater part of the country. Imago, end of July to August. Full grown larva, June. Larvae of these beetles feed openly on the roots. The adults feed on the leaves.

(40) *Longitarsus gracilis* Kuts.

(41) *L. suturellis* Dup. (*thoracicus* Steph.); and

(42) *L. ochroleucus* Marsh., are also recorded from ragwort.

Records of Coleoptera from Fowler, *Coleoptera of British Isles*, etc.

(iv) HEMIPTERA.

Pentatomidae.

(43) *Pentatoma rufipes* L.: imago, end of June to October. On flowers of ragwort. General throughout British Isles. Other hosts: *Quercus*, *Crataegus*, *Fraxinus*, etc.

Coreidae.

(44) *Therapha hyoscyami* L.: imago, August–September. Swept from flowers. Near Pendine, near sea. Other hosts: *Ononis*, *Erodium*, *Hyoscyamus*, etc.

Berytidae.

(45) *Berytus signoreti* Fieb.: imago, March–October. From roots. Northumberland—Gloucester, Herts, Surrey, Berks, etc. Other host: *Erica tetralix*.

Tingidae.

(46) *Monanthia ciliata* Fieb.: imago, April–June. Under ragwort in sandy places. Oxon, Berks. Other hosts: *Ajuga reptans*, *Verbascum*, etc.

(47) *Monanthia simplex* H.S.: imago, May–August. Bucks, Kent, Surrey, Hants, Devon. Also under *Euphorbia cyparissias*.

Capsidae.

(48) *Phytocoris ulmi* L.: imago, June–October. All over Europe. Other hosts: *Ulmus*, *Prunus*, *Betula*, *Acer*, *Alnus*, etc.

(49) *Calocoris bipunctatis* Fabr.: imago, June–October. All over Europe. Other hosts: *Vicia sativa*, *Carduus*, *Papaver*, etc.

(50) *Neocoris bohemani* Fall.: imago, July–August. Cheshire, Kent, Devon, and nearly whole of Europe. Other host: Sallow. On thistle and ragwort, probably casual occurrences.

Coccidae.

(51) *Targionia nigra*: at base of woody stem. France, Corsica, Italy, Algeria, etc. Other hosts: *Cineraria maritima*, *Fagonia cretica*, *Genista delphinensis*, etc.

Aphididae.

(52) *Aphis rumicis* L.: June–July onwards. Europe generally, Africa, India, etc. Forty-seven other hosts (*Artemisia*, *Carduus*, *Pyrus*, etc.).

(53) *Aphis jacobaeae* Schrk.: common June and July. Wye, Herne Bay, Germany, Belgium, etc.

(54) *Anuraphis cardui* L.: July–September. General over England and Wales, Europe, America. Other hosts: *Carduus* spp., *Senecio* spp., *Chrysanthemum*, etc.

(55) *Anuraphis helichrysi* Kalt.: June–Autumn. Great Britain, Ireland, Europe, etc. Other hosts: plum, damson, etc.

Records of Hemiptera mostly from Butler, *Hemiptera-Heteroptera*.

(v) THYSANOPTERA.

Thripnoidea.

(56) *Haplothrips distinguendus* Uzel.: adults from end of June to October. Eggs laid amongst flowers. North-east Scotland and Southern England, etc. Ragwort true host plant.

At least twenty-one other species of Thysanoptera are found on ragwort, many of which are merely casual visitors, while others may breed on the plant, although they have many other hosts, and yet others may occur in great numbers on the weed but do not breed on it. Among the latter are *Physothrips atratus* Hal., *P. vulgatissimus* Hal., *Thrips flavus* Schrank. and *Thrips fuscipennis* Hal. The occasional breeders on ragwort are *Aelothrips fasciatus* L., *Aptinothrips rufus* Gmelin var. *stylifera* Trybom and *Thrips tabaci* Lindeman.

After a preliminary survey, taking into account the effective damage produced by the various species and the specificity of their food habits, two insects were selected for special study; the Ragwort Moth or Cinnabar (*Tyria jacobaeae*), belonging to the family Arctiidae, and the Anthomyiid fly, *Pegohylemyia seneciella* Meade.

Several other species, which do minor damage to ragwort, have also received some study. Among these may be mentioned *Agromyza aeneiventris* Flin., a

dipterous stem borer, *Homeosoma nimbella* Dup., a lepidopterous stem borer, *Phytomyza atricornis* Mg. and *Spilographa zoe* Loew., leaf-miners, and an aphid, *Aphis jacobaeae* Schrk.

(c) *The two important insects.*

A. *Tyria jacobaeae* L.

(i) *Synonymy, description, and distribution.*

Tyria (*Hipocrita*, *Euchelia*, *Callimorpha*) *jacobaeae* L. is a member of the family Arctiidae (Lepidoptera). Meyrick describes it in *British Lepidoptera* as follows:

“Head, thorax, and abdomen black. Forewings blackish grey; a crimson subcostal streak from base to $\frac{5}{8}$, extremity expanded; a crimson dorsal streak from base to $\frac{2}{3}$; a crimson dorsal spot below the apex, and another above the tornus. Hindwings crimson; a costal streak, middle of terminal edge, and cilia blackish grey. Wing spread 35–45 mm.”

The species occurs commonly throughout Britain, its range extending as far north as the Caledonian Canal, although it is scarce north of the Clyde. It is also common in Ireland. In Europe it occurs as far east as, and including West Central Asia.

(ii) *Life history.*

The adult. In England the moths emerge from the hibernating pupae about mid-May, and become more plentiful throughout the latter half of May and June. The eggs are laid on the under-surface of the leaves of *Senecio jacobaea* L., and occasionally on *S. vulgaris* L. (groundsel), to which two plants the species is confined in nature. In tests, the larvae have also been found to feed on *S. cineraria*, the garden cineraria. The eggs are deposited on the under-surfaces of the lower leaves of ragwort, in clusters, containing from one to 130 or more, though the clusters usually contain from thirty-five to forty-five eggs. Occasionally there may be more than one cluster on a leaf. The eggs, which measure 0.65 mm. in diameter, are yellow, and faintly reticulated. Before hatching, the chorion, through which the black cuticle of the larval head can easily be seen, changes from yellow to a glistening greyish colour. In the field incubation requires approximately 13 days, while in the incubator, at a temperature of 23° C., the eggs hatch in 5 days. The average number of eggs laid by a female is about 200, the lowest number laid by those under observation being ninety-eight, and the highest 301. In one case observed, oviposition proceeded as follows:

Moth paired on 13th June, 1930.

14th June, 1930	...	29 eggs laid
16th June, 1930	...	181 eggs laid
19th June, 1930	...	91 eggs laid
Total		301

The larva. The eggs hatch out about the end of May, or later, according to the season, and larvae are common throughout June and the greater part of July, except in a late season like 1932, when they were scarce until the end

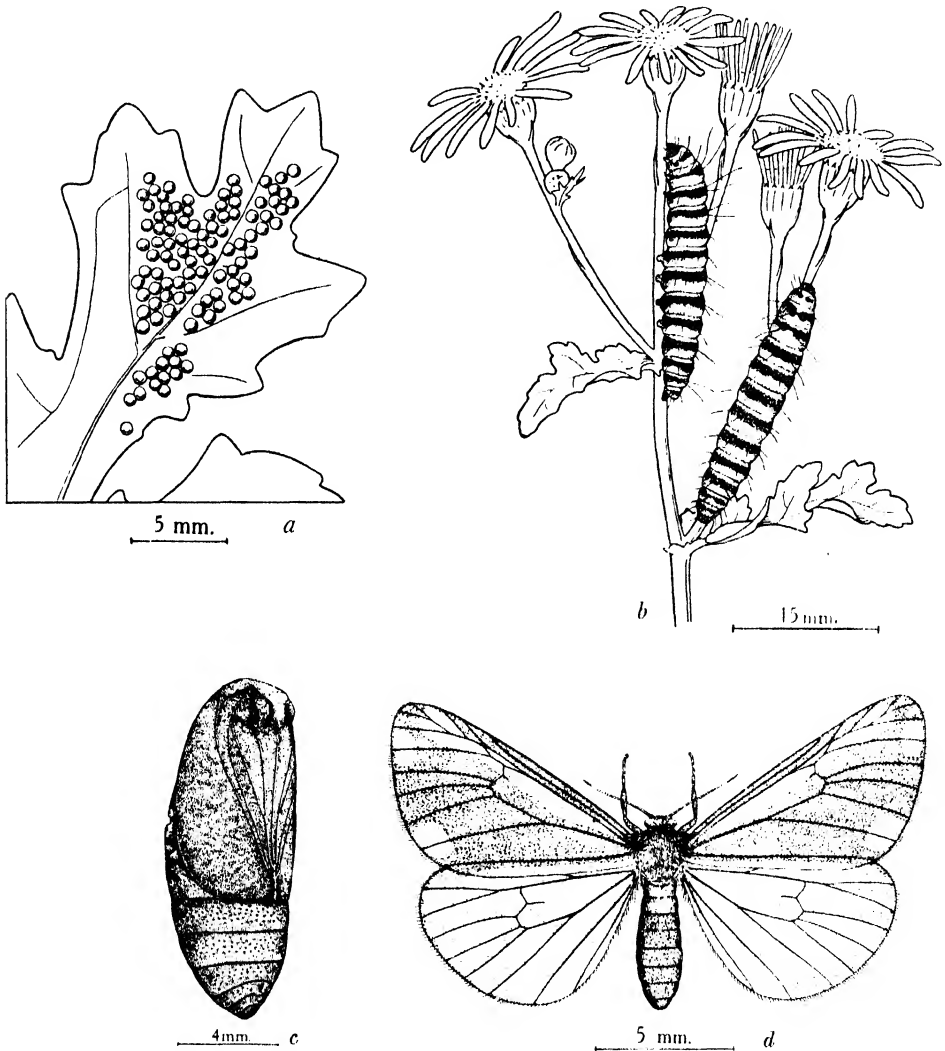


FIG. 4. *Tyria jacobaeae* L.: a, eggs on under side of ragwort leaf; b, larvae; c, pupa; d, adult with wing venation emphasised.

of June. Towards the end of July they prepare to enter the pupal stage. There are five larval stadia. The first instar is greenish yellow in colour, with an arrangement of black dots on the tip of the hair papillae. On the third day after hatching, the general effect is deep yellow with black dots. The second instar, which appears 5–6 days after hatching, is striped, black bands alternating

with narrower bands of a greyish green colour. After 3-4 days in this instar the ground colour becomes yellow, with a regular arrangement of black dots. About the tenth day after hatching the larva enters the third stadium, when it assumes the characteristic yellow and black bands of the two remaining stages.

The following table gives the various measurements of each instar, and the length of each stadium:

Instar	Length mm.	Breadth at middle mm.	Breadth of head mm.	Length of stadium days
1	2.09	0.45	0.385	5-6
2	4.00	0.75	0.600	5-6
3	8.00	1.30	0.942	5
4	13.00	2.20	1.430	5
5	15.50	3.70	2.010	10-11
Mature 5	25.00	5.00	2.010	—

The larval period occupies just over one month. The head measurements in the successive stages agree with Dyar's Law, the mean ratio being 1.51.

During June and July, in the south of England, the larvae of the cinnabar may be seen in certain areas in countless thousands, rapidly eating up the flowers, leaves, and top parts of the stems of ragwort. At Henley-on-Thames a ragwort area had a population of twelve larvae per plant, or nearly one and a quarter millions per acre. Over large regions in Norfolk they were equally abundant. In fact they are a feature of the Breckland area of this county, and are so numerous in some parts that they find their way into the cottars' houses in search of suitable places for pupation. Sometimes a road intersects a ragwort area, and the larvae, or canker-worms as they are locally called, in crossing from depleted ragwort to fresh plants on the other side, get killed in thousands by passing motor cars.

The pupa. The insect enters the pupal stage towards the end of July or a few weeks later, according to the season. A few odd larvae remain on the plants for several weeks after the main batch has pupated. When the fifth-stage larva is fully fed, it seeks out some protected position under moss, grass, small stones, or just beneath the soil surface. Here it may form a very imperfect cocoon with the aid of soil and a slight webbing, but this is often absent. When the last larval skin is moulted, a bright yellow pupa is formed, which, if touched, is capable of slight movement. In the course of 24 hours it hardens, the colour becoming reddish, and gradually darkening to reddish brown. In this stage the insect passes the winter.

In length, the pupa measures about 11.5 mm., while at its middle it is 5 mm. broad.

Testing of Tyria. An extensive series of larval tests was carried out in order to find out if *Tyria* can attack other plants. The selected plants were lettuce, chrysanthemum, sunflower, golden rod, aster, Michaelmas daisy, and dahlia. Negative results were obtained, none of these plants being eaten by the larvae. This part of the work was carried out at Rothamsted by Mr J. C. F. Newton.

(iii) *Parasites of the eggs and larvae.*

The following parasites of *Tyria jacobaeae* L. are recorded in the literature. Those of which the names are in brackets have not been reared by me, and are probably extremely rare:

HYMENOPTERA.

Braconidae:

1. *Apanteles popularis* Haliday.
2. (*Apanteles difficilis* Nees.)

Ichneumonidae:

3. (*Ichneumon* (*Cratichneumon*) *Gravenhorsti* Fusc.)
4. (*Melanichneumon saturatorius* Thoms.)
5. (*Mesostenus obnoxius* Grav.)
6. (*Spilocryptus incubitor* Strom.)
7. (*Spilocryptus migrator* Fab.)
8. (*Cryptus obscurus* Grav.)
9. (*Erigorgus insidiator* Forst.)
10. (*Labrorhynchus tenuicornis* Grav.)
11. (*Exetastes illusor* Gr.)
12. *Mesochorus facialis* Bridg.
13. (*Mesochorus anomalus* Holmgr.)
14. (*Hemiteles fulvipes* Grav.)

} Hyperparasites of *Apanteles popularis*

DIPTERA.

Tachinidae:

15. (*Tachina macrocera* Rob. Desv.) (*Tachina nitidiventris* Zett.)

Very few of these parasites were obtained from English material, though an immense number of *Tyria* larvae and pupae were reared. On the other hand, several new parasites were reared, and added to the list.

Egg parasites. Although very many thousands of eggs were collected in the Farnham Royal area and allowed to hatch, no parasites were obtained. A number of eggs were exposed to attack by the Chalcid egg parasite *Trichogramma* sp., which has many lepidopterous hosts, but negative results were obtained. One per cent. of the eggs collected in the field were sterile.

Parasites of the larvae. (1) *Apanteles popularis* Hal.—Braconidae (Microgasteridae). During 1930, 1931, and 1932, several thousand *Tyria* larvae from different areas in Buckinghamshire, Oxfordshire, Surrey, and Norfolk, were dissected for parasites. The first and second stage endoparasitic larvae of this Braconid, with the characteristic caudal vesicle, were obtained in the following numbers: 1930, 4 per cent.; 1931, 5 per cent., one area in Surrey—Wentworth—had 19 per cent.); 1932, 41 per cent. This variation in the percentage of parasitism from year to year was also noted by Lyle, who in one year found a 60 per cent. attack, and in the following year, in the same area, no attack. Daviault, in 1928, found that 40 per cent. of the caterpillars were attacked by *A. popularis* in the sand-dunes at Wimereux, near Boulogne.

This parasite is gregarious, several larvae inhabiting a single *Tyria* caterpillar. The highest number found was fifteen, while the average was five. The adults emerge from their cocoons during the first weeks of July, and proceed to parasitise the early stages of the *Tyria* caterpillars. The larva, when fully fed (towards the end of July), emerges from the mature fifth stage *Tyria* caterpillar, and hibernates inside a tough, woolly, white cocoon, pupating

shortly before the appearance of the imago. The cocoons are arranged in irregular groups of 6-9, and are connected with each other by a few threads.

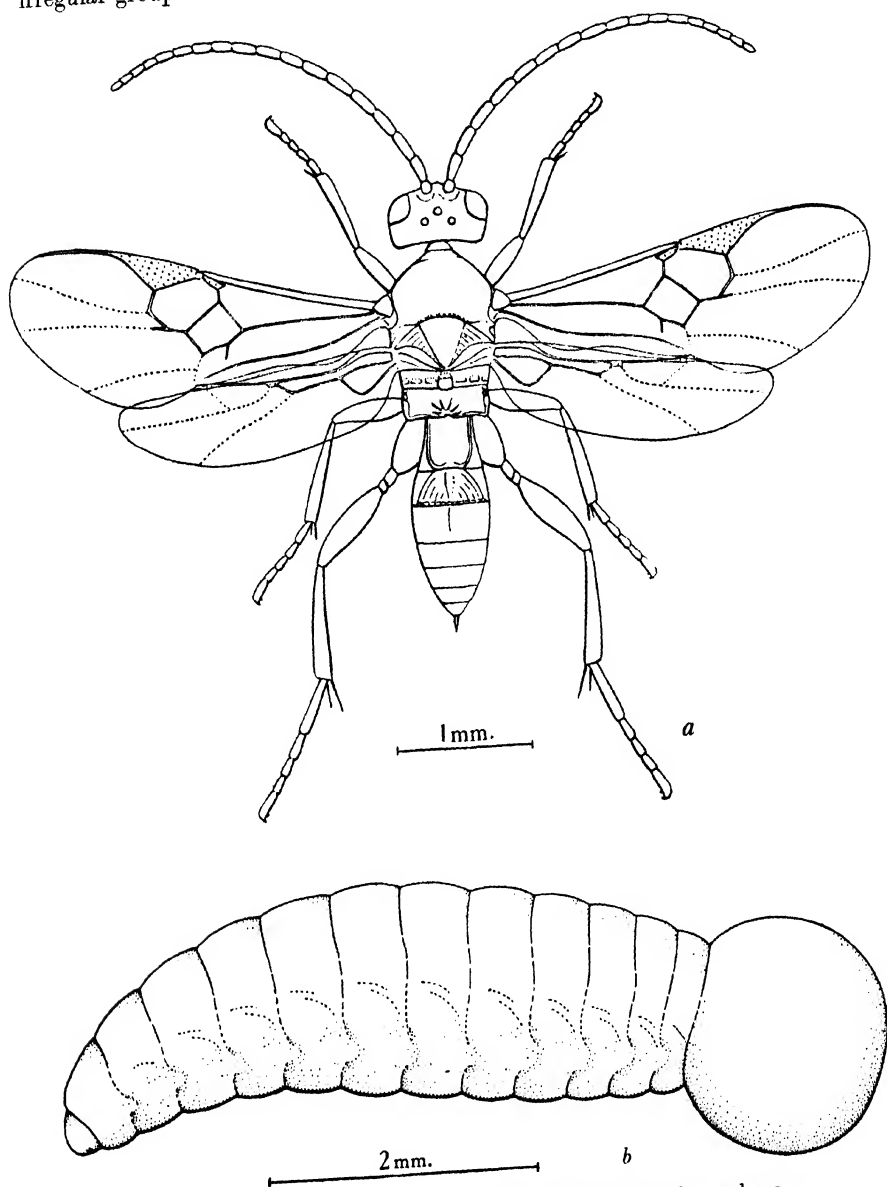


FIG. 5. *Apanteles popularis* Hal.: a, adult female; b, second stage larva.

A rather inadequate description of the biology and larval stages of this species has been given by Daviault.

(2) *Mesochorus facialis* Bridg.—Ichneumonidae (Ophioninae). The larvae of this hyperparasite were dissected from the last stage larvae of *Apanteles popularis* Hal., removed from living caterpillars of *Tyria* and found to occur in the following numbers: Buckinghamshire, 60 per cent.; Norfolk, 15 per cent. *Mesochorus* is a solitary parasite.

(iv) *Parasites and predators of the pupae.*

(1) *Ichneumon* (*Melanichneumon*) *perscrutator* Wsm. (Ichneumonidae—Ichneumoninae). Several thousand of the pupae of *Tyria jacobaeae* L., collected in large quantities from Norfolk during the seasons of 1929, 1930, 1931, were dissected in order to ascertain the percentage infestation by this solitary

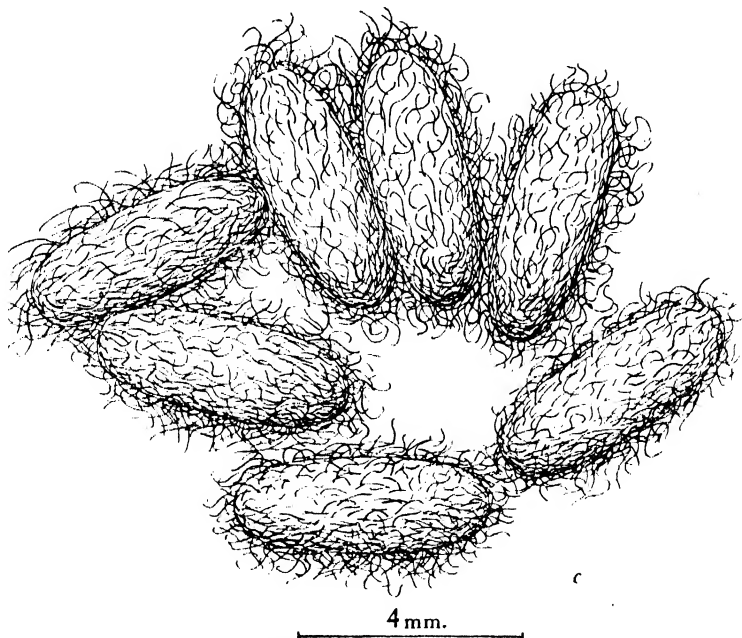


FIG. 5. *Apanteles popularis* Hal.: c, cocoons.

parasite. In 1929 this amounted to 15 per cent., but in the following years, 1930, and 1931, it fell to 2–3 per cent. This sudden drop might have been attributed in part to the large collection of 1929, with its accompanying reduction in the ichneumon population, were it not for the fact that the infestation outside the collecting areas was similarly 2–3 per cent. Other factors must therefore contribute to this violent fluctuation in the numbers of the parasite.

As far as I am aware this is the first rearing record of *Ichneumon perscrutator* Wsm.

(2) *Psychophagus* (*Diglochis*) *omnivorus* Walk. (Chalcidoidea—Pteromalidae). During the first collecting season (1929–30), the larvae of this parasite were obtained by dissections of the host, and the adults bred in large

numbers from *Tyria* pupae. Although very abundant, the actual loss which the *Tyria* population incurred as a result of its activities was relatively small—due to its superparasitic habit. As many as forty-four or more adults issued from a single *Tyria* pupa, while the average number of parasite larvae in an infected pupa was about thirty-two. The infestation in the main collection averaged 3–4 per cent. One lot of 200 pupae had fifty-four (or 27 per cent.) infested. In the two following collecting seasons (1930–1, 1931–2) the infestation by *Psychophagus* was practically nil.

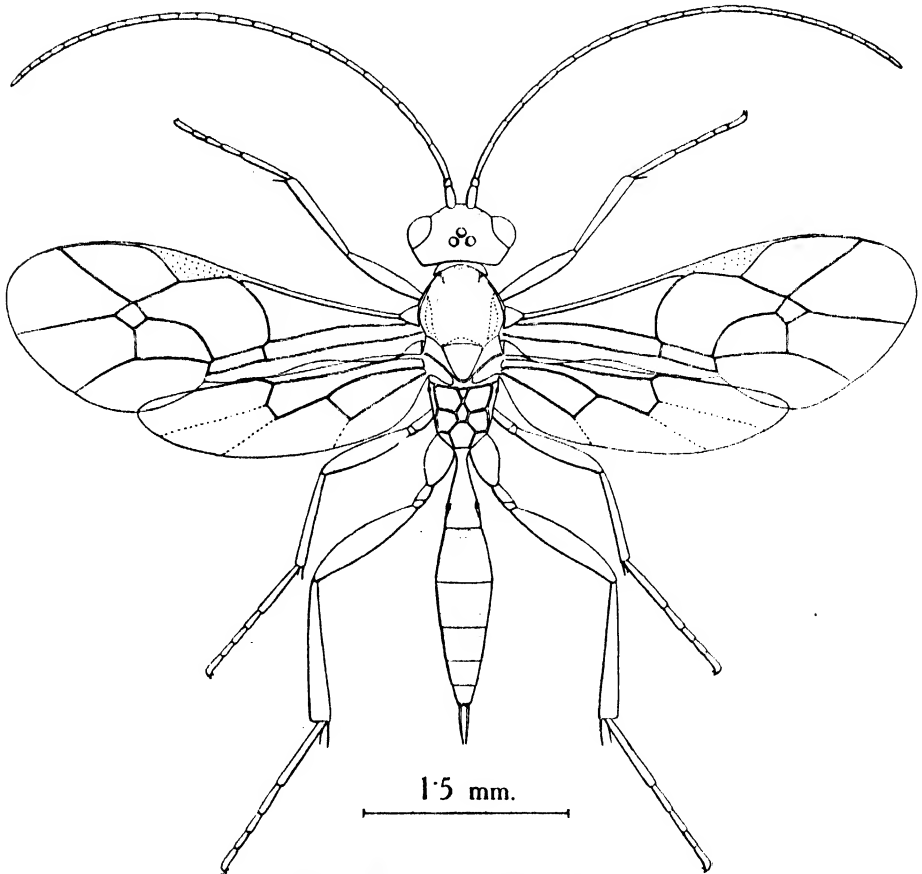


FIG. 6. *Mesochorus facialis* Bridg. ♂.

A few specimens of the following were also reared from *Tyria* pupae:

Ichneumonidae:

Cryptinae: *Hemiteles* sp.

Pimplinae: *Pimpla instigator* F.

Chalcidoidea:

Chalcididae: *Brachymeria minuta* L.

Pteromalidae: *Coelopisthia vitripennis* Thoms.

Fungus parasites of the pupae. The pupae of *Tyria jacobaeae* suffer rather heavily from the attack of various species of fungi. An attempt was made to isolate and identify each species. For this purpose two media were employed: potato-dextrose agar, and malt and meat extract. Both gave good results. Another method which did away with the necessity for cultivation media, consisted in taking a small piece out of the integument of each of a hundred pupae with a pair of forceps, sterilising the instrument in a flame after each

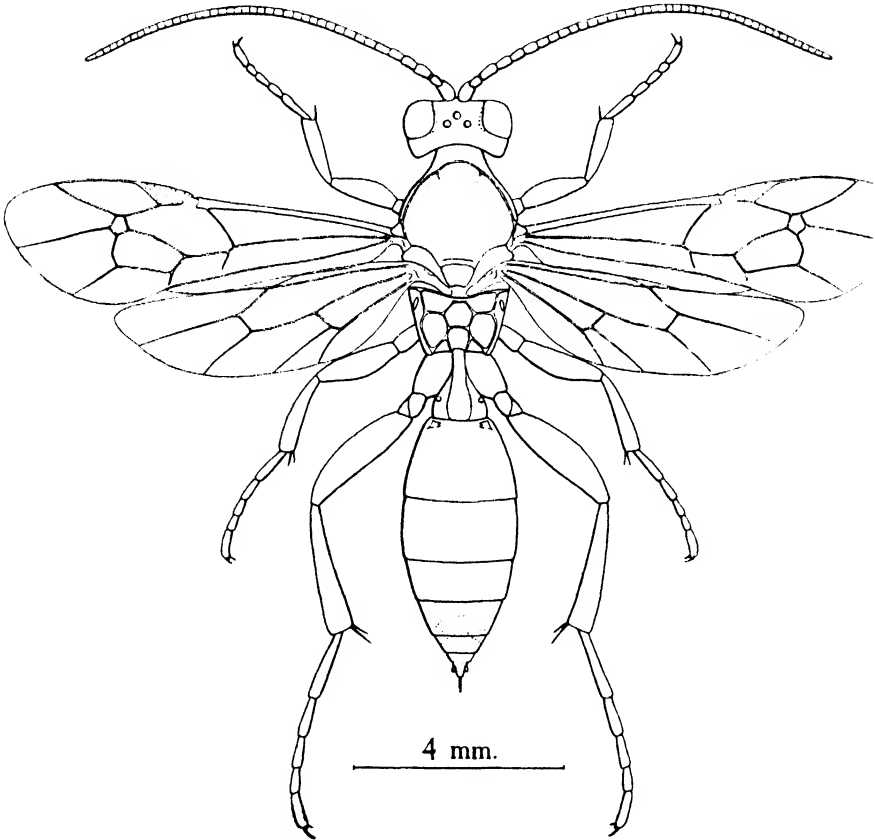


FIG. 7. *Ichneumon perscrutator* Wsm. ♀.

operation. The pupae were then placed on a tray containing damp sterilised sand or moss, and the whole covered with a bell-jar. Under such ideal conditions, any fungi present in the pupae soon grew out of the openings and were then ready for identification.

Towards the end of the 1930-1 period, the following fungi were isolated and identified, from pupae collected at Stanford, Norfolk:

<i>Isaria farinosa</i>	Infestation	...	10.5 per cent.
<i>Fusarium</i> sp.	Infestation	...	7.7 per cent.
<i>Beauveria Bassiana</i>	Infestation	...	0.5 per cent.

Collections of pupae were made in the Norfolk area as opportunity offered throughout the pupal periods of 1929-30, 1930-1, and 1931-2. Several thousand dissections were made, and the average percentage mortality caused by the combined attack of these fungi ascertained. In 1929-30 this mortality was equal to 16 per cent. in the earlier part of the pupal period (August-May), increasing towards the end to 20-22 per cent.; in 1930-1, 5 per cent. in the earlier period, increasing to 19 per cent. in the later, and in 1931-2, 16-18 per cent. in the middle of the pupal period.

The results thus obtained show that *Tyria* in the pupal stage is subjected to an annual loss of 16-20 per cent. of its population from the combined attack of the fungi cited.

Predators of Tyria pupae. Since the larvae of *Tyria* are distasteful to birds, and are further protected from attack by their yellow and black warning colours, the effect of predators is felt only in the pupal stage.

Several experiments were conducted during the winter of 1929-30, to ascertain the percentage of mortality in *Tyria* pupae, resulting from the action of predators. These experiments were made in Norfolk, over 100 miles distant from the Laboratory, consequently they were rather limited. Nevertheless, although general conclusions cannot be drawn from them, they serve to show that the mortality in the pupal stage from various predators is considerable.

An area in Breckland, in which the natural population was found to be approximately 25 pupae per 100 sq. ft., and which had a large quantity of denuded ragwort stems, was chosen and a number of plots pegged out. Three of the plots measured 10 ft. by 10 ft. (100 sq. ft.). In each of these twenty-five pupae were placed in small groups under stones, simulating, as closely as possible, the natural position and numbers. Two further plots, measuring 1 ft. by 1 ft., were made in a mossy area, and forty-eight pupae were placed under the surface of the moss at equal intervals in each. Near these, on open soil, two exactly similar plots were prepared, and pupae, at the rate of forty-eight per plot, placed at equal intervals on the soil surface.

These plots were prepared about the end of October and examined at the beginning of December, about five weeks later. The mortalities observed were as follows:

Mortality in the plots with pupae under stones	...	65 per cent.
Mortality in the plots with pupae under moss	...	69 per cent.
Mortality in the plots with pupae on soil surface	...	90 per cent.

The experiments thus indicate that the effect of predators in reducing the numbers of *Tyria* in the pupal stage is very great. At least 60 per cent. were accounted for in this manner in the area under review—Stanford, Norfolk. The pupae occur most generally under moss and small flat stones, which are abundant in Breckland. Very occasionally they may be found on the soil surface.

Observation and experiment indicate that the following animals may be listed as probable predators: moles, mice, crows, rooks, and game birds. Fed to pheasants the pupae were eaten sparingly; partridges also ate them. The most important predator is probably the mole. In several plots mole runs were discovered under the stones where pupae had been placed, and from all these the pupae had disappeared. Again in certain areas, where *Tyria* was known to be pupating, the soil was riddled with mole runs, and in such areas pupae were very scarce, although there had been an abundant supply of larvae. Crows and rooks have been observed in the distance foraging on the pupal grounds, but we have, as yet, no definite proof that they feed on *Tyria*.

B. *Pegohylemyia seneciella* Meade.

(i) *Synonymy and distinctive characters.*

During the course of the weed-control investigations, a large number of Anthomyiid flies were bred from the capitula of ragwort from various areas in England and Scotland. They were kindly determined by J. E. Collin, a specialist in the group, as being chiefly *Pegohylemyia seneciella* Meade, with a few specimens of *P. jacobaeae* Hardy. *Chortophila* and *Phorbia* are synonyms of *Pegohylemyia*. The females of *P. seneciella* and *P. jacobaeae* are very similar, but Collin has found differences in the tibial bristles and the arista; they can be distinguished as follows:

<i>P. seneciella</i>	<i>P. jacobaeae</i>
1. No preapical bristles on hind tibiae	Three strong preapical bristles on hind tibiae, just above tarsus
2. Arista not so pubescent as in <i>jacobaeae</i>	Arista more pubescent than in <i>seneciella</i>
3. General colour usually dull grey	General colour usually more golden grey

Characters 1 and 2 also apply to the males, but these can easily be separated by colour differences, *seneciella* being much darker (almost black) than *jacobaeae* (grey-black).

The genitalia also differ, but as Mr Collin has prepared a paper, to be published shortly, dealing fully with the systematics and differences of these two species, I do not intend to deal further with them.

(ii) *Life history.*

The fly begins to make its appearance during the last week in June, coincident with the time when ragwort capitula are beginning to expand, and from the end of June onwards it is fairly common.

The eggs are laid both in the expanded and closed capitula, well down between the bases of the florets, usually one per capitulum, though very occasionally two eggs may be found in the same capitulum. The egg is white in colour, smooth, and glistening, oval in shape and tapering towards both ends. Its length is 0.84 mm., its breadth, at the middle, 0.28 mm. The incubation period is short, hatching taking place 3 or 4 days after oviposition.

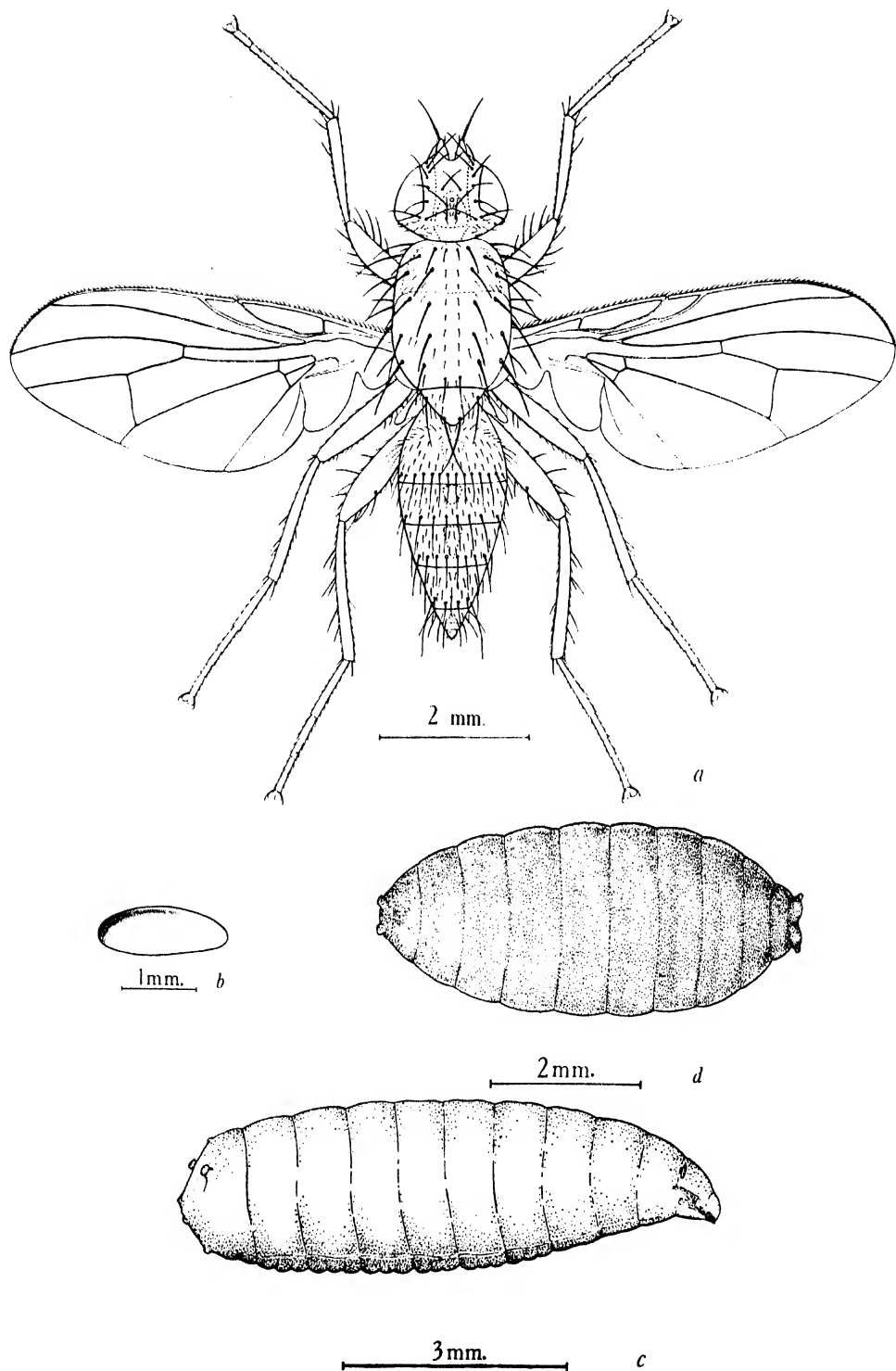


FIG. 8. *a*, *Pegohylemyia seneciella* Meade; *b*, egg; *c*, mature larva; *d*, puparium.

There are three larval instars, maturity being reached towards the end of August in the south, and later further north. In Ross-shire, Scotland, it is as late as the end of September. On maturity the larvae drop from the flowers and pupate in the soil. Mature larvae measure 7 mm. in length, puparia 5.5 mm.

Ragwort capitula infested with the larvae of *Pegohylemyia* are easily detected, on account of the dark brown central spot which characterises them. This diagnostic spot grows larger with the larvae, and is due to two causes: the withering of the florets in the region of the larva's activities, and the dirty colour of the matted florets, which the larva forms round itself as a kind of protective tube. This matting is probably helped by the extraction of a kind of cement from the tissues of the plant.

The larva eats the immature seeds, and part of the base of the involucre towards which end of the flower its head is directed. The percentage of infestation of, and the amount of damage caused by this insect, is discussed under the section dealing with the survey of insect damage.

(iii) *Parasites.*

A large number of larvae of *P. seneciella*, collected in the Farnham Royal area, were dissected for parasites. A solitary Braconid larva was found in 51 per cent. of the maggots. This parasite was later reared and identified as *Phaenocarpa ruficeps* Nees.

The following parasites were reared from the puparia:

- | | |
|----------------|--|
| Braconidae: | <i>Phaenocarpa ruficeps</i> Nees. |
| Ichneumonidae: | |
| Cryptinae: | <i>Hemiteles fulvipes</i> Grav. (hyper.) |
| Chalcidoidea: | |
| Pteromalidae: | <i>Lamprotatus splendens</i> Westw. |
| | <i>L. obscurus</i> Walk. |

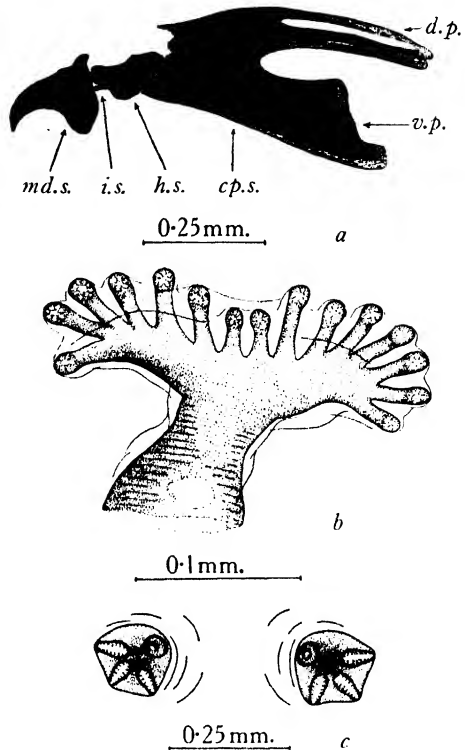


FIG. 9. *Pegohylemyia seneciella* Meade: *a*, buccal pharyngeal apparatus of mature larva; *b*, anterior spiracles of mature larva; *c*, posterior spiracles of mature larva. *md.s.*, mandibular sclerite, *i.s.*, interstitial sclerite, *h.s.*, hypostomal sclerite, *cp.s.*, cephalo-pharyngeal sclerite, *d.p.*, dorsal process of cephalo-pharyngeal sclerite, *v.p.*, ventral process of cephalo-pharyngeal sclerite.

(d) Biology of other ragwort insects.

During the course of the investigations, several insects were observed to be causing damage to ragwort, but not in sufficient number to be of significance in the control of the plant. A few brief notes on these are included here:

(1) *Agromyza aeneiventris* Flh. This Agromyzid fly bores in ragwort stems, tunnelling the pith and reducing a great deal of it to frass. It also appears to do some slight damage to the adjacent layers of parenchyma. The imago, a small shining black fly, is a very common and pretty insect on ragwort from June onwards. Both larval and pupal stages are passed in the pith of the stem.

An estimation of the percentage larval attack, and of the numbers of larvae per infested stem, was made at Wentworth, Surrey; Hambledon, Bucks; Henley, Oxon; and Dorney, Bucks. At Wentworth, 31 per cent. of the stems examined were found to be infested, the average number of larvae per stem being three. At Hambledon, a 41 per cent. infestation was recorded, with a similar larval average of three per stem. At Henley and Dorney the infestation was 100 per cent., while the average number per stem at Henley was nine, and at Dorney 5.3. From these figures it will be seen that the fly is quite common on ragwort, but owing to the fact that its attack is confined chiefly to a non-vital part of the plant, the pith, its value as a controlling agent is relatively small.

The following parasites were reared from the puparia:

Chalcidoidea:

Pteromalidae: *Sphegigaster aculeatus* Wlk.

Syntomopus thoracicus Wlk.

Cleonymidae: *Caudonia agylla* Walk.

Cynipoidea:

Eucoelini: *Diglyphosema conjungens* Kieff.

Parasitism by the Cynipid, *Diglyphosema conjungens* Kieff., which has previously been recorded only from France, thus making the genus new for Britain, reached 15-17 per cent.

Other parasites of this fly recorded in the literature are as follows:

Braconidae: *Dacnusa rufipes* Nees, from Europe.

D. senilis Nees, from France.

Gyrocampa senilis Nees, from Germany.

Ichneumonidae: *Phygadeuon rusticellae* Bridg., from Germany.

Carduus nutans L., *Cirsium lanceolatum* L. (Scop.), and *C. eriophorum* L. (Scop.), are also recorded as hosts of *Agromyza aeneiventris* Flh.

(2) *Homeosoma* (stem-borer). A number of ragwort stems was kindly sent to me on September 15th, 1930, by Dr A. S. Watt of Cambridge, who collected them on the sand-dunes at Dornoch, Sutherlandshire. On examination they were found to be infested with a stem-boring lepidopterous larva. The collar

of the root was also observed to be attacked. Out of twenty single-stemmed plants, fourteen were found to be infested, thirty larvae in all being recovered, thus giving an average of two larvae per stem, and an infestation of 70 per cent. The plants were rather inferior specimens, such as one would expect from a sand-dune area, and appeared to have suffered rather badly as a result of boring attack. According to Dr Watt, the ragwort over a large area of the dunes seemed to be dying as a result of the infestation by this insect.

A single specimen was bred through and identified as *Homeosoma nimbella* Dup., a moth of the family Phycitidae. The following parasites were also reared:

Ichneumonidae:

Pimplinae: *Glypta rufata* Bridg.

Pimpla inquisitor Scop.

Two other species of *Homeosoma* are known to occur on ragwort in Britain---*H. cretaceella* Rossl. and *H. nebulella* Hubn.

In New Zealand another species is already active---*Homeosoma vagella* Zell. The infestation of this moth in certain areas is reported to be as high as 80-90 per cent., and in others 100 per cent. It does not appear to have any controlling effect on vigorous plants, but in one area an important result of its activities was noted. On a farm were two paddocks, a few hundred yards apart, both containing ragwort which had been cut down once. In one, the infestation by *vagella* equalled 100 per cent., and in the other only 40 per cent. Where the borer had been particularly active in the 100 per cent. paddock, no secondary growth took place, whereas in the 40 per cent. paddock secondary growth was vigorous. The absence of secondary growth in the former was attributed to the effect of *vagella* on the crown of the roots, which were found to be largely rotted. If this insect is widespread, and an effective check to secondary growth, it should prove an important ally and auxiliary of *Tyria* in the control of ragwort.

It is, however, evident that, since New Zealand has already a lepidopterous stem-borer of the genus *Homeosoma*, there can be no further need for investigations on the allied British species, especially as the amount of damage caused by the British species does not seem to be greater than, if as great as, that already occasioned by *H. vagella*.

(3) *Leaf-mining Diptera*. Two species of leaf-mining Diptera have been recorded from ragwort---*Phytomyza albiceps* Fln., and *P. geniculata* Macq., both belonging to the family Agromyzidae. The common species observed and reared from ragwort in the South Bucks area is *Phytomyza atricornis* Mg. This species makes a narrow linear mine about 1 mm. wide, extending generally over the upper surface of the leaf. The egg, which is whitish grey in colour, and twice as long as broad (breadth 0.33 mm.), is laid in the leaf. The larva emerges in about 3 or 4 days. At Farnham Royal an average of three larvae per leaf was obtained. When fully fed it pupates generally on the under surface

of the leaf, just underneath the lower epidermis. Several generations occur in a year.

From the puparia the following parasites were reared:

Chalcidoidea:

Eulophidae: *Chrysocharis syma* Walk.

Braconidae: *Dacnusa arcularis* Nees.

Three further parasites are recorded in the literature:

Eulophidae: *Chrysocharis elongatus* Thoms. and *Solenotus viridis* Forst., both from Serbia.

Braconidae: *Paxilomma buccata* Breb., from Europe.

Another species which makes very much larger, irregular, blotchy mines is the Trypetid, *Spilographa zoe* Loew. The Chalcid parasite, *Lamprotatus obscurus* Walk. (Pteromalidae), has been reared from the puparia of this fly.

(4) *Sphenella marginata* Flin. This Trypetid fly was reared from a quantity of flower-heads collected in Norfolk, to obtain the emergence of mature *Pegohylemyia* larvae.

(5) *Aphis jacobaeae* Schr. This aphid is very occasionally found in clusters round the upper part of the stem of ragwort.

(e) *Survey of insect damage, with notes on plant reaction to attack.*

(i) *Method of study.*

Senecio jacobaea L., is a common weed throughout Britain. The two insects proposed for its control, *Tyria jacobaeae* L. and *Pegohylemyia seneciella* Meade, are distributed as follows: *Tyria* has a range extending from the south coast of England to the Caledonian Canal in Scotland. It is very plentiful in the south, in ragwort-infested country, but is scarce north of the Clyde. *Pegohylemyia*, on the other hand, is fairly well distributed throughout the country, from north to south, large collections having been made in Ross-shire, Scotland, not far from the northern seaboard. In some regions, however, its distribution is rather local.

A special study of the damage caused to ragwort by these insects was made in several areas in Buckinghamshire, Norfolk, Oxfordshire, and Surrey, England, while further notes were made on the activities of *Pegohylemyia* in the counties of Aberdeen and Ross, Scotland.

Some of these areas, having a fairly high infestation of ragwort, and being more or less removed from the routine of cultivation, which would have broken the natural sequence of events, as well as from interference from members of the public, were studied as "Type Areas". The populations of type areas were ascertained by means of a collapsible wooden square, each side of which measured 4 ft., giving a total area of 16 sq. ft. In taking the census several transects, 4 ft. wide, were made across the area in different directions. From figures obtained in this way, the population of ragwort plants per acre

was calculated. For seedlings, because of the difficulty of accurately counting the tiny plants, a smaller square, with 2 ft. sides, was employed.

A census similar to this was made of all the type areas. In following up the course of ragwort control by insects and other factors from year to year, a table of the following kind (with modifications to suit each area), providing, as it does, all the necessary data for quick and accurate comparison of different types of infestation in the field, is invaluable.

Area: Fawley Court Hill, Henley-on-Thames, Oxon, England. (Approximately 12 acres.)

Date of original survey: July 6th, 1931.

Type: Deer Park, overgrazed; occasional oak trees.

Soil: poor.

Altitude: 35 ft.

Association: chiefly grasses; permanent meadow.

Distribution: regular.

Mature plants per square yard: 22.

Mature plants per acre: 108,900.

Seedlings per acre: 152,460.

Plant type: Average height: 2 ft.

Range: 10 in., 1 ft., 2 ft., 3 ft. 8 in.

Average number of stems per plant: 1.

Average number of capitula per stem: 68.

Average number of seeds per capitulum: 70.

Average number of seeds per plant: 4760.

Larvae of *Tyria jacobaeae*: 1,216,800 per acre; 11 per plant.

Pegohylemyia: nil.

Other insects: *Agromyza aeneiventris* Fln. (stem-borer), common. *Aphis jacobaeae*: very occasional.

(ii) *Nature of Tyria attack and reaction of ragwort.*

The larvae of the cinnabar devour leaves, flowers, and part of the stems of ragwort. When the attack is really severe, as it nearly always is, an area of ragwort in full flower, such as the one we have just described, with 108,900 plants per acre, and 1,306,800 for the whole area of 12 acres, may be reduced to bare stems. Such reduction actually occurred in the two seasons of 1930 and 1931. A good idea of the havoc which is wrought by *Tyria* can be gathered from the illustration (Pl. XXI, phot. 2).

Superficial observation of a ragwort area after the deadly attack of the cinnabar, would naturally lead one to the conclusion that complete suppression and extinction of the weed must necessarily follow this entire destruction of leaves and seeds. Not so! Ragwort is possessed of recuperative powers, which can, and do, partly negate this result.

The reaction of the ragwort takes the form of secondary growth. When

healthy, vigorous plants are cut down in the early flowering stage, a number react by sending forth new shoots from the old stem. These ultimately produce a new crop of flowers, which later give rise to seeds. Failing this production, the crown of the root may become active, and begin to send forth small shoots, which, in the following spring, after the old stem has decayed, grow out to form a new plant. If the season is unfavourable, very little of either type of secondary growth takes place. It is a fairly general rule, however, in a good season, for attacked plants to make a second attempt at reproduction in one or both of the ways just described (Pl. XXI, phot. 3).

In addition to the observations made on the form and amount of this growth, following on *Tyria* attack, a number of experiments on the effect of wholesale and progressive cutting of ragwort, designed to simulate insect attack, were carried out. From these experiments, results comparable with those following true insect damage were obtained.

The first experiment in this direction was carried out at Wentworth, Surrey, on fairly good land left derelict for future building purposes. Ragwort was present on this area to the extent of 40,000 plants per acre. On July 3rd, 1930, several acres of these plants, having an average height of 4 ft. 1 in., and an approximate seed number of 115,240, were mowed down to within 2-4 in. of the ground. Nearly 4 months later (October 31st, 1930), the field was again a mass of ragwort flowers, except for a control area of several hundred square yards, where a large number of uncut plants had attained maturity and seeded, during the first fortnight of September, about six weeks previously. These control plants were now dried up and withered, whereas the new shoots and flowers produced secondarily from the bases of the cut plants were still fresh.

A comparison of seed yields, height, and time of flowering, of the attacked and unattacked plants follows:

	Uncut plants	New growth of cut plants
Height	4 ft. 1 in.	2 ft.
Number of stems	10	15
Capitula per stem	179	40
Seed yield	115,240	39,945

The seeds of the uncut plants ripened during the first fortnight in September, while those from the secondary growth of the cut plants did not attain maturity until the end of November. From this experiment, carried out over an area of 5 acres, the following conclusions were drawn.

The cutting of strong healthy specimens of ragwort to within 4 in. of the ground, shortly after the flowers have opened (when *Tyria* attack is commencing) results in:

(1) The production of secondary shoots which produce flowers, and ultimately seeds.

(2) An increase of 50 per cent. in the number of stems, the average thickness of the new stems being half that of the old.



Phot. 2. Illustrating the effect of *Tyria* larvae on Ragwort. Left - normal Ragwort plant; right - plant entirely denuded by caterpillars.



Phot. 3. Illustrating plant reaction to attack. Left - flowering Ragwort plant; right above - cut to within 4 inches of ground; right below - secondary growth from base of cut stem.

(3) A secondary seed yield equal to 34·7 per cent. of the yield potentially producible, in the absence of attack.

(4) A retardation of seed ripening by 10 weeks.

The next experiment consisted in the progressive cutting of transplanted ragwort in the Laboratory garden. From one lot all the leaves were removed, from another all the capitula, and from the remainder, all leaves, flowers, and top portions of the stem. In interpreting the results of this experiment, the condition of the plants must be considered. They had been transplanted in the late rosette stage and as a result had used up some of their reserves in becoming established, so they are equivalent to plants which are none too vigorous, growing on poor soil, with little reserve food to draw on in case of emergency.

The lot having all leaves removed produced a number of small new leaves. The seed yield was reduced by 10 per cent. Those with all the flowers nipped out produced a new lot of capitula. The seed yield was reduced by 60 per cent. In the remaining lot, where leaves, flowers, and the top part of the stem were cut off, no reaction took place and the plants died.

From this series of experiments on wholesale and progressive cutting of ragwort, we may draw the following main conclusions, which were confirmed by further observations in the field:

(1) A badly attacked plant, if originally vigorous and if the growing season is good, has enough reserve energy to produce a second crop of seeds equal to 34·7 per cent. of the original potential yield producible in the absence of attack, thus reducing a total loss of 100 per cent. to one of 65·3 per cent.

(2) Plants with little or no reserve energy, growing on very poor soil, when badly attacked, do not produce seeds secondarily.

(3) Many plants which are not able to produce a second crop of flowers and seeds in the year of attack may send out small shoots from the base of the stem. These shoots grow vigorously in the following year, and are often capable of producing more seed than the original plant. Field observations show that this method of secondary growth has the effect of prolonging the life of the plant beyond the ordinary biennial period.

(4) Damage to any part of the plant, leaves, stem, and flowers, will lower the seed yield for that season.

Passing on to the consideration of actual attack by *Tyria jacobaeae*, we find these results verified.

At Henley-on-Thames, ragwort, infesting 12 acres of deer-pastured meadow, was found to be heavily attacked by *Tyria*. On July 11th, 1930, all the plants had been eaten leaving bare stems. On September 12th, 1930, when the area was re-visited, numerous secondarily produced flowers were observed, the field being a mass of yellow flowers. Calculations revealed that the seed yield from this secondary flower growth was equal roughly to 35–40 per cent. of the potential seed yield, a result similar to that of the large-scale cutting

experiment at Wentworth. This same area in 1931, after similar heavy *Tyria* attack, had only an occasional plant reproducing secondarily. Such a condition can be accounted for by the unfavourable season, and the consequent reduction of reserve food supplies.

At Wentworth A area, Surrey, an area with medium sized, not very vigorous plants was kept under observation. A plot, 16 sq. ft. in area, was mapped out, and the following notes made:

July 3rd, 1930. Number of plants: 14.

Average height: 2 ft.

Average number of *Tyria* larvae per plant: 15.

Approximate total number of larvae: 210.

Estimated seed yield per plant: 20,000.

Estimated seed yield for area: 280,000.

On September 12th, 1930, all fourteen plants were eaten to bare stems by *Tyria* larvae and eight showed initial secondary growth, with a new seed production of (1) 4020, (2) 2680, (3) 938, (4) 804, (5) 2010, (6) 1675, (7) 670, (8) 835; i.e. a total of 13,632 seeds. The estimated seed yield in the absence of attack was 280,000 seeds, while the actual yield produced secondarily was 13,632 seeds. This means a conversion of a 100 per cent. loss to a 95 per cent. loss.

Another similar plot had a secondary seed production of 12,199, and an estimated seed yield of 270,000, again a conversion of a 100 per cent. loss to one of 95 per cent. In this area the plants were of poor quality, and lacking in reserves, hence the drop in secondary yield as compared with the Henley area.

* Another plot at Littleworth gave results similar to Wentworth A area. This plot had an area of 1296 sq. ft., with thirty-six plants, averaging 2 ft. 3 in. in height. The estimated potential seed yield was 381,900. After a heavy attack by *Tyria* secondary growth produced 19,263 seeds. This is equal to 6 per cent. of the potential seed yield, or a 94 per cent. loss.

An even more impoverished area with poorer plants was observed at Stoke Poges:

Size of area	136 square yards
Number of plants	14
Height	2 ft. 6 in. to 3 ft.
Estimated seed yield for area	331,650

On July 29th, 1930, all fourteen plants were reduced to bare stems by *Tyria*. Observations were made up to November 20th, 1930, but no secondary growth occurred. Therefore seed loss was equal to 100 per cent. Reserve food in this area, either in the plant or in the soil, was reduced to a minimum, so that the infestation was wiped out.

These various experiments on the reaction of ragwort to cutting, and to insect attack, clearly illustrate one important way in which the biological control of noxious weeds differs from the biological control of noxious insects.

In the case of the insect pest, the damage produced by a single parasite is normally sufficient to destroy its host. In the case of a plant pest like ragwort we have to reckon with a reactive power for reproduction, which partly nullifies the destructive effectiveness of the natural enemy feeding on it. This reactive power is absent in the insect. Its absence, coupled with the greater ease with which an insect can be killed, accounts for the greater success in insect control work.

(iii) *Effectiveness of Tyria as a control.*

From superficial observation of the tremendous havoc which *Tyria* causes amongst ragwort infestations, one might come to regard this moth as an ideal control, were it not for the fact that in many of these devastated ragwort localities the infestation often proves to be as high in the year following the attack. This is due, as we have already seen, largely to secondary growth. On the other hand, secondary growth does not always occur. It does not occur in an unfavourable season even in fairly vigorous plants, and it rarely occurs, even in a good season, in inferior plants growing on poor and ungenerous soils. Under these two sets of conditions, *Tyria* is an effective control.

The area at Fawley Court Hill, Henley, will illustrate the effectiveness of control when secondary growth, owing to the unfavourable season, was eliminated.

On June 21st, 1932, this extensive type area of 12 acres, which in 1931 had a population of 108,900 mature plants per acre, or 1,306,800 for the whole area, and 152,460 rosettes per acre, or 1,529,520 for the whole area, was observed to be entirely free from mature ragwort, except for about a dozen scraggy plants, 6 in. high, at one corner. Young plants were also absent from the whole area, except for one or two odd specimens. In 1931, *Tyria* attack on this area was considerable, there being approximately 15,681,000 larvae on the area, or an average of twelve per plant. Owing to the unfavourable season of 1931, no secondary growth took place, and, consequently, there was no seed to produce seedlings in 1932¹. Those actually occurring must have arisen from a few odd seeds which escaped the ravages of *Tyria*. The wholesale clearance in 1931 of the ragwort leaves, seeds, and top parts of the stems, coupled with the absence of secondary growth, resulted in the apparently very satisfactory control.

On the day the field was visited (June 21st, 1932), a large number of *Tyria* moths was seen flying about, seeking in vain for plants on which to oviposit.

The natural sequence of events in this area appears to be that *Tyria*, owing to the absence of food plants, will very largely die out. To prevent reseeding of the area from the outside, certain precautions, which will be dealt with

¹ In 1930 the attack of *Tyria* on this area was tremendous, equal in intensity to that of 1931; nevertheless, the area maintained, in 1931, a population of over 100,000 plants per acre, similar to that of 1930. This population was produced (in the favourable season) from a secondary crop of seeds, and from secondary growth at the base.

later, must be taken. Effective control was also brought about by *Tyria* at Stoke Poges, where a small infestation of ragwort, growing on very poor soil, was exterminated.

After observations over a wide area, the following conclusions have been drawn regarding the effectiveness of *Tyria* as a control:

(1) Provided that the attack is general (see "Types of Land" (3), p. 309) and that no secondary growth follows, either in the shape of a new crop of flowers, or of new growth from the base, to carry the ragwort over into another year, *Tyria* can be a very effective controlling agent.

(2) When poor plants, growing on very inferior soil, are heavily and uniformly attacked by *Tyria*, the ragwort infestation should be wiped out.

(3) Once an infestation is under control, certain precautions have to be taken in order that the area may be kept free of ragwort. These take the form of (a) stimulation of grasses in the area, (b) avoidance of overgrazing, etc., and are discussed in a later section.

(iv) *Effectiveness of Pegohylemyia as a control.*

Pegohylemyia is an internal capitulum feeder. The eggs are laid amongst the flowers in the expanded and half-opened stage, usually one per capitulum. On emergence the larva commences to eat the seeds. The infested florets are easily recognised by a brown spot in the disc, which grows larger as time goes on. This is due to the premature withering of the central flosculi. As the larva feeds, it mats some of the florets around it, probably as a protection from parasites. Sometimes it pierces through the receptacle into the stalk.

In order to ascertain the extent of the infestation of this fly, and the amount of damage which it causes, ragwort flower heads were examined from various areas throughout Britain, among which may be mentioned Stanford, Norfolk and Medmenham, Bucks, in England; and Banchory, Aberdeen, and Achterneed, Ross-shire, in Scotland.

Material examined at Banchory, Aberdeen, on August 30th, 1930, was found to have 21·8 per cent. of the capitula infested with the larvae of *Pegohylemyia*. 70–75 per cent. of the seeds of each infested capitulum had been destroyed.

At Stanford, Norfolk, the infestation per 100 capitula was only 8·7; at Medmenham, Bucks, 8·5; while at Achterneed, Ross-shire, Scotland, the peak figure of 33·7 was reached. The percentage of seeds eaten by each larva was about 70–75 per cent. of each capitulum, a capitulum averaging roughly seventy seeds.

The position of *Pegohylemyia* as a control is as follows: in Southern England it infests approximately eight to nine of every 100 capitula, and in the capitulum attacked, 75 per cent. of the seed is destroyed. In Northern Scotland its capacity as a destructive agent to the seed output appears to be much greater, for it attacks approximately thirty-three or thirty-four out of

every 100 capita. The northern range of this insect, so far as larger numbers are concerned, is much greater than that of *Tyria*, which does not extend much further north than the south of Scotland (found sparsely as far north as the Caledonian Canal), so that *Pegohylemyia* has the advantage of 200 miles, or even more to the northern limit. This advantage may perhaps be useful in New Zealand in higher and colder regions, where it may be impossible to establish *Tyria*.

(v) *General survey of ragwort control in Britain.*

A brief description of the main types of ragwort infestations in this country, where some degree of control has been effected, will indicate how the work should progress at the other end.

In Britain three main types of land have been observed in connection with ragwort control by insects:

(1) Good farm land. Ragwort is controlled on this type of land by proper cultivation, coupled with the maintenance of a good turf and the avoidance of overgrazing.

(2) Poorer land, with ragwort in comparatively small areas, isolated from extensive ragwort country. As we have already seen (pp. 306, 307), ragwort infestations have been controlled in areas of this type by *Tyria*. Once control is attained in such areas, the problem is to effect its continuance. If a field is isolated from other ragwort by woods and good farm land, a lot of seed should not find its way in from outside. However, in order to forestall the fulfilment of such a possibility, the pasture grasses must be given a chance to come away strongly, so that they may form a soil covering, sufficiently dense to preclude the re-establishment of ragwort seedlings. This could be effected in three ways: firstly, by the prevention of grazing for a period; secondly, by stimulation of the grasses present with artificial manures, such as lime and basic slag, etc.; and, thirdly, by killing rabbits and other animals which expose the soil surface, thereby providing ragwort with a suitable seed bed.

In some areas, such as part of Stoke Poges already referred to, the land is so extremely poor and hard that the plants never acquire sufficient vigour to reproduce themselves secondarily: consequently *Tyria* attack is very effective. Owing to the infertility of the soil, it is not possible to maintain a close uniform cover of grass, so the measures proposed in the preceding case are inapplicable or unnecessary. When present, *Tyria* ought to be quite effective by itself on land of this sort.

(3) Extensive ragwort country, many square miles in area, where the soil is poor and much of the surface exposed by direct and indirect rabbit activity, provides ideal conditions for the establishment of ragwort seedlings. Much of the Breckland of East Anglia, which in addition to rabbit-exposed soil has large areas of derelict arable land, too unproductive to reward further cultivation, is of this type. Several factors militate against the achievement of

control by *Tyria* in this desolate country. *Tyria*, although widespread, is only locally abundant. Consequently, when small areas, with badly attacked ragwort showing no signs of secondary growth, are brought under control, as at Henley, they become supplied with new seed from the unattacked ragwort, which has a plentiful supply for dispersal. In this manner the ragwort is maintained in the area.

The real stabilising factor of the infestation, however, is rabbit activity, which has caused a break in the plant community, with consequent exposure of the soil surface. If rabbits were to be excluded from this region, the natural succession of plants which occupied the derelict areas prior to cultivation would gradually cover the soil and effectively prevent the establishment of ragwort seedlings, so that the infestation would come to an end. This has already taken place in certain areas of Breckland.

Therefore, to anyone attempting to control this weed, we cannot too strongly emphasise the importance of eliminating factors (such as rabbit activity, and overgrazing by farm animals), which predispose to open soil conditions.

One way of dealing with a poor unproductive area like Breckland would be to lay it down to forest. Several large portions have already been planted by the Forestry Commission with Scots pine, etc., not for the purpose of controlling ragwort, although it has done this very effectively, but in order to make use of waste land, and to build up a reserve of timber for the future.

VI. THE ECOLOGY AND CONTROL OF RAGWORT IN NEW ZEALAND.

(1) BIOLOGICAL CONTROL.

The control of ragwort in England has been discussed in Part v. In New Zealand conditions are somewhat different. The Dominion is essentially a grazing country, and cultivation occupies a minor place in the work of the farmer. On the better class farms, where the land is good, ragwort is kept under control as it is under similar conditions in Britain. It is on the poorer types of pasture land, and on the large areas of bush grasslands, where cultivation has never taken place, that ragwort is a menace. Possibly two other factors, in addition to the absence of the insect fauna, enter into the explanation of the ragwort problem of New Zealand. These are the poor quality of the soil, especially in the North Island, which has had to import many millions of tons of phosphates to improve it, and the unorthodox method of pasture production (i.e. sowing on burnt-over areas which have not been ploughed) with the establishment of poor strains of grasses and clover.

A complex of four main insects will be concerned in the efforts to effect some sort of control of the ragwort pest. These are:

Tyria jacobaeae L. (introduced): seed- and leaf-eater.

Nyctemera annulata Boisd. (native): as *Tyria*.

Pegohylemyia seneciella Meade (introduced): seed-eater.

Homeosoma vagella Zell. (native): stem- and crown-borer.

In New Zealand the following native insects are recorded from ragwort:

Lepidoptera. *Nyctemera annulata*: attacks leaves and flowers.

Homeosoma faranaria: stem-borer.

H. vagella: stem-borer.

Diptera. *Agromyza* sp.: pith-borer.

Phytomyza affinis: leaf-miner.

The Lepidopteron, *Nyctemera annulata* is attacked by the Ichneumonid, *Echthromorpha intricatoria* F., and by the Tachinid, *Lydella* (*Phorocera*) *casta* Rond.

Tyria, *Pegohylemyia*, and *Nyctemera* will deal with the seeds as effectively as they can. When secondary growth follows in their train their work will be partly nullified. This may be partly obviated by the work of *Homeosoma*, boring in the crown of the roots and preventing any new growth. If conditions turn out to be similar to those of the Henley area, where no new growth took place in an unfavourable season, progress will be quicker and easier.

Whether *Tyria* and *Pegohylemyia* will be more effective in New Zealand than in Europe it is impossible to say. It was hoped at one time that in the warm New Zealand climate *Tyria* would pass through two generations in a season and thus increase greatly in destructiveness; but up to the present there has been no change in its life history. It may be also that *Tyria* will suffer less from parasitic attack in New Zealand than in Europe (though two parasites of a very common native Noctuid, *Nyctemera annulata* Boisd.—which also feeds on ragwort—have already attacked it; one species, the Tachinid *Lydella casta* Rond. in the larval stage, the other, the Ichneumonid, *Echthromorpha intricatoria* F. in the pupal stage), but the possibility of ragwort being favoured by the milder climate and longer growing season, with a greater likelihood of secondary growth, might outweigh this advantage.

(2) OTHER METHODS OF CONTROL.

(i) *Cultural methods.*

On the better class farms of Britain, ragwort is successfully controlled or prevented from obtaining a footing by good cultivation and the maintenance of good pastures. This may be described as the preventive method, and is undoubtedly the best one. In areas where the land is of poorer quality, or on farms where the management is not so efficient as it ought to be, or again on dairy pastures where the land is kept under grass for a long period of years, with overgrazing, the stimulation method of control may be employed. This consists in the treatment of the pastures with suitable fertilisers. A good turf is the result, and this will effectively prevent seedling establishment. The existing ragwort plants must, of course, be removed entirely, root and stem.

The experience of a Sussex farmer with this method may be cited. When he took over a farm of 300 acres, the grassland was heavily infested with

ragwort, "as thick as corn in some fields". During the first summer he mowed it down, but this process, according to neighbouring farmers, had not hitherto proved successful. In November, an application of 5-6 cwt. of basic slag to the acre was made and the grass harrowed. At the end of three years, 200 acres of the grassland had been slagged. Results in the summer following on the first application proved the method, on the worst land, to be a success. This farmer continued to dress his land with slag every other year, until at the end of 10 years ragwort was entirely eradicated, and the farm was able to support twice as much stock as it did prior to the application of fertilisers.

To accelerate the process, the mature ragwort plants, at the time of commencement of fertiliser application, and in the following year, should be entirely removed. This process is known as "stubbing". A sharpened hoe or a small spade with a keen edge is used as a stubber, and with either of these implements the entire plant is removed. A number of rootlets occasionally get left behind, and these, it is said by farmers, may produce new plants in the following year. A second round with the stubber will get rid of these and the fertiliser part of the method will effectively prevent the establishment of seedlings.

Another method of getting rid of the mature plants is to pull them up by hand, after rain has softened the soil. Still another method is to mow down the weed at certain periods of the year, when the plant is just coming into flower, and when the secondary growth has been fully formed. According to the experience of several farmers, this type of control is not very effective unless carried out over a period of years.

(ii) *Grazing.*

The importance of preventing overgrazing by stock, if ragwort is to be excluded from the composition of the pastures, has already been emphasised. For a comprehensive account of the management and care of pastures, the reader is referred to books like *Range and Pasture Management* (by A. W. Sampson—John Wiley and Sons, Inc., New York, 1923), etc. Davies in "Grazing" (*Bull. Bur. Pl. Genet.*, Aberyst., No. 10, 1933) gives the following advice for the maintenance of a good pasture: "Controlled intermittent grazing at all times of the year; the length of the rest period and the intensity of grazing to be determined by the pasture type concerned, and the demands of the species which it is desired to encourage."

The method of ragwort control by stocking infested pastures with sheep has long been known. It has proved very successful, but unless certain precautions are taken, a high mortality amongst the sheep may ensue. Cattle and horses will not eat ragwort unless forced to do so, but sheep are very fond of it, especially when it is in the young rosette stage. Although they are fairly tolerant to the poisonous principles of the weed, long-continued feeding on ragwort alone will ultimately prove fatal.

It is necessary, then, when this type of control is to be tried out on pastures heavily infested with ragwort, to divide the fields up into small areas, so that the weeds in each area are very closely eaten. The sheep must be transferred occasionally to weed-free pasture or else a high mortality will occur.

Old ewes are much less susceptible to ragwort poisoning than are the younger animals, hence they have been employed more successfully. As well as this greater degree of tolerance to the poison, they have an added advantage in that they attack the crown or growing region of the rosette, whereas the younger sheep eat the outer leaves. The attack on the crown is more quickly and more certainly effective.

Ragwort control by means of sheep should be carried out during the late winter and early spring, when the weed is in the rosette stage. It is then succulent and inviting, while the pasture is uninviting. At this stage too, the plant contains a smaller proportion of poisonous alkaloids. Sometimes sheep are allowed to feed continuously on ragwort when it is in full bloom. This procedure is invariably followed by fatal results. On dairy farms liable to a slight or moderate ragwort infestation, it is a good plan to allow a few old ewes to graze along with the cattle throughout the year. They will successfully keep the pasture free from ragwort.

(iii) *Application of chemicals.*

During the last few years various experiments have been carried out by the New Zealand Department of Agriculture, to test the effectiveness of the chlorates of sodium and calcium in weed control. Ragwort, because of its abundance and menace to dairy farmers was chosen for prior treatment. Both chlorates successfully killed the weed, but for various reasons sodium chlorate was found to be more suitable for use, and at the same time its killing properties were proved to be stronger than those of the calcium salt. On the other hand, sodium chlorate presents a risk of fire. When clothes which have become wet with the spray are dried, they ignite easily when placed near an open flame. A French preparation of the salt, "Occysol", obviates this fire risk, while, at the same time, its effectiveness in killing the weed is equal to 98 per cent. of that of the pure chlorate.

Sodium chlorate can be used for killing ragwort either in the dry crystalline state or in the form of a spray solution. The solution is preferable, one of 3-5 per cent. concentration giving a 100 per cent. kill. The plants should be sprayed during the winter and spring, when they are in the rosette stage; a 4-5 per cent. solution is then advisable. When the plants are entering the flowering stage a 2 per cent. solution is strong enough. Although the mature plant thus appears to be receiving a much smaller amount of chlorate, in reality it may be receiving more than the rosette, for it requires a much larger amount of the solution to wet it.

The spray does not affect grass, nor is it poisonous to stock. It does,

however, render the weeds more attractive to stock, who may eat them and suffer from ragwort poisoning. Care must be taken then, for a short period, to prevent the animals from gaining access to the sprayed weeds.

Another chemical preparation tested for ragwort control was a mixture of common salt, three parts, and iron sulphate, one part. This is applied in the dried state and is effective for small infestations.

VII. MASS COLLECTIONS AND SHIPMENTS OF WEED-CONTROLLING INSECTS.

During the course of the ragwort, gorse, and blackberry control investigations, the writer collected nearly three-quarters of a million insects for shipment to New Zealand. Out of this number, about half were intended for the control of ragwort.

The collection of suitable insects for shipment in large quantities is one of the major problems of a weed control project. A great deal of time, trouble, and money was spent on this branch of the work.

Tyria jacobaeae L. The chief collecting area for pupae of the cinnabar is situated in East Anglia, in the Breckland region of the county of Norfolk. The Breckland consists of huge areas of unproductive soil, strewn with small flints; in fact it is an area partially approaching the steppe type. At one time portions of this land had been enclosed from ancient commons, and ploughed or broken up (Breck = broken), hence the name Breckland. The ploughed areas ultimately proved unproductive and were largely allowed to return to their natural state. They are occupied in places by heather, bracken, and dwarf grass vegetation. Some of the Breck associations are made up of the grasses *Festuca ovina*, *Agrostis tenuis*, and *Aira praecox*; the mosses *Hypnum cupressiformae*, *H. schreberi*, *Hylocomium triquetrum*, *Leucobryum glaucum*; and other plants including *Galium verum*, *G. saxatile*, *Alchemilla arvensis*, *Rumex acetosella*, *Urtica dioica*, *Dactylis glomerata*, *Potentilla erecta*, *Sedum acre*, *Cerastium vulgatum*, *Cirsium* spp., etc. In certain areas of the wastes of the open dwarf grass association, large quantities of ragwort are found.

In addition to the permanent Breck, there are areas of agricultural land, which, owing to the poor returns for cultivation, have been left derelict by the farmers and are gradually reverting to the Breck type. Ragwort is usually abundant on such land.

The soil of the Breckland is light, chalky, and sandy, and receives an annual rainfall of 22.5 in., one of the lowest in England. Such a country offers an excellent opportunity for the establishment of ragwort, ultimately because of its soil and climate, and immediately because of the relative openness of the vegetation, and because of the greatly diminished plant competition. The openness of the vegetation is intensified by the burrowing of innumerable rabbits, which create additional suitable seed beds for the establishment of ragwort seedlings.

Headquarters for the collection of pupae were established at Stanford, a lonely hamlet in the wilds of Breckland. Work began about the end of July and continued throughout August. Collecting proved to be a slow business, until speeded up by the employment of local workers, chiefly women and boys, to whom payment was made at a given rate per thousand. The procedure involved in the collection was as follows. First of all, the country was explored by car, in order to locate suitable collecting grounds. Although the characteristic alternating yellow and black banded larvae were very numerous in many areas, suggesting an easy and plentiful supply of pupae, the finding of areas where the latter might be obtained in sufficient quantities to warrant the transportation of workers to them, was often very difficult. In some places where numerous small flints were scattered over the ground, the collection, though slow, was easier. These stones were turned over, and under the smaller, flatter types, pupae were often found in nests of 1, 2, 3, or 4, and occasionally 6 or 7. When supplies from this source were exhausted, resort was made to the grassy and mossy parts of the area. The grass and moss were pulled up in handfulls, and grubbing in the surface layer of the soil revealed the pupae.

The daily collections were brought back to headquarters, stored in appropriately ventilated boxes, with damp moss as packing, and conveyed periodically to the laboratory by car. On arrival at Farnham Royal, the pupae were sorted prior to shipment. All malformed and small specimens, also those of a dull black colour, which were usually parasitised or attacked by fungi, were discarded. Only healthy looking pupae of a bright reddish brown colour were selected for shipment. The pupae were finally packed in small tin boxes, with slightly damp sterilised sphagnum as packing material, the moss providing the requisite humidity. These tins were also packed with sterilised sphagnum, in larger wooden boxes, and were then ready for shipment.

Shipments were made from the Royal Albert Docks in the boats of the Shaw, Savill, and Albion Shipping Co., and the New Zealand Shipping Co., whose agents were very helpful in making arrangements for the conveyance of the insects in the vegetable chamber of the various vessels concerned. A fairly equable temperature of 34 to 38–40° F. was maintained in these rooms, so the pupae were unaffected by the greater variations of temperature experienced on the voyage. On arrival at Nelson, New Zealand, the shipments were met by an official of the Cawthron Institute, previously advised by cable, and the insects conveyed to the quarantine insectaries, there to await further testing and ultimate liberation.

An attempt was made to send eggs of *Tyria*, but none of these hatched after their arrival in New Zealand. In all, 294,382 *Tyria* pupae were exported to New Zealand.

Pegohylemyia seneciella Meade. Different methods of collection were employed for this insect. Owing to the smallness of the puparia, no attempt was made to collect in this stage, as the numbers so recoverable, after the

expenditure of a great deal of time and labour, would have been negligible. The material was collected in the late larval stage. The florets of ragwort infested by the larvae of *Pegohylemyia* were easily distinguished by the dark brown central spot on the disc, which became larger as the larvae grew older. The time for collection was determined by the size of the larvae. When they were considered to be nearly mature, the heads of the plants with a fairly high infestation, were collected *en masse*, and packed in sacks. At the end of the day the sacks were despatched by passenger train to the laboratory. In

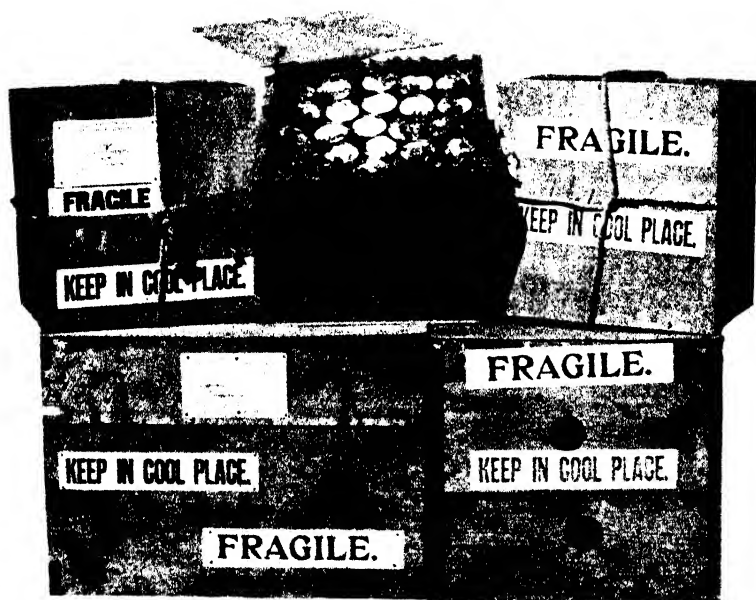


FIG. 11. Consignment of ragwort control insects ready for export to New Zealand.
Top centre box open to show packing method.

making these collections two main points had to be kept in mind: first the actual time for collection is very short, as the larvae, when mature, quickly drop to the ground for pupation and so are lost; and secondly, collection of the larvae before maturity is attained, will result in undersized puparia. Thus it will be seen that for a successful collection of *Pegohylemyia*, one must be on the alert for the critical stage. This insect was collected in Norfolk, North Lincolnshire, and Yorkshire, while a number were sent from Ross-shire in Northern Scotland.

On arrival at the laboratory, the flower-heads were spread out on trays in the insectaries. Daily collections of larvae and puparia were made from

the bottoms of the trays, and the final selection of puparia packed in tin boxes with slightly damp sphagnum moss, in the manner already described for *Tyria*. A total of 58,000 puparia of *Pegohylemyia* was shipped.

While the ragwort investigations were proceeding, shipments of gorse and blackberry insects were made from time to time.

Apion ulicis Forst. Shipments of this gorse-controlling beetle were made in the adult stage. At first they were collected by beating the gorse bushes and allowing the various insects to fall into nets held underneath. The Apions were then separated from the conglomerate mass of pods, thorns, and various insects, by means of sucking tubes.

Later, in order to maintain the absolute purity of the species, gorse pods, containing mature *Apion* larvae, were collected from the gorse bushes in August. These were spread out in cages in the insectary, where on reaching maturity, the weevils, being themselves unable to force a way out, were liberated when the pods burst, as a result of the drying action of the sun's rays. The beetles thus collected were placed in muslin bags, containing gorse twigs, which had their ends waxed to conserve moisture and freshness. A number of these bags were then placed in adequately ventilated wooden boxes for final shipment.

In all 273,260 individuals were shipped to New Zealand.

Coraebus rubi L. This Buprestid beetle, intended for the ultimate control of blackberry, was collected in the Antibes area of Southern France. The collection was carried out by a field agent in the *Coraebus*-infested rose nurseries of that region, where the insect is so injurious that many nurserymen are reported to be going out of business owing to its attacks. During the autumn and winter months the rose stocks containing larvae of *Coraebus* (identified by cutting a thin slice from the side and so revealing the brown galleries of the root-boring larva), were collected and sent in cane hampers covered with sacking, to Farnham Royal. At the laboratory they were examined and repacked tightly in wooden boxes, for export to New Zealand.

In all 7647 infested rose stocks were shipped, thus bringing the grand total of selected insects for export to 633,289.

SUMMARY.

1. Ragwort (*Senecio jacobaea* L.) was introduced into New Zealand from Europe prior to 1874, since when it has become a very serious pest in the Dominion. Its wide and rapid spread was attributed to the absence of the European insect fauna, which exercised a controlling effect on the weed in its native lands. Accordingly, the present investigation was undertaken in order to discover the factors, insect or otherwise, which kept ragwort under control in Britain, with a view to their ultimate utilisation in suppressing the pest in New Zealand.

2. The paper opens with an account of the initiation of the New Zealand Noxious Weed Control Scheme, and a summary of previous attempts to subjugate weeds by the biological method.

3. The main principles underlying the biological control of weeds are summarised and the procedure to be followed in work of this kind indicated. One of the dangers in weed control by insects is the possibility that the introduced species may migrate from the weed to plants of economic value. With proper safeguards this risk is greatly minimised. Several experiments dealing with this problem are quoted, and the subject discussed.

4. Ragwort is described in its various stages, while details of the life history of the weed, the history of its introduction into New Zealand, its botanical status, relation to plants of economic value, its poisonous properties, together with the diseases which it causes in stock are fully related.

5. A fairly complete ecological study of ragwort, showing the effect of climatic, edaphic, and biotic factors on the establishment and distribution of the weed, reveals the biotic factor to be of the greatest importance in its control. The effect of plant competition on the establishment of the seedling is extremely important. Long grass and short continuous turf prevents the establishment of ragwort altogether, while overgrazed pastures, owing to the partial exposure of the soil surface, carry a high infestation of the weed. *Man*, *Insects*, *Sheep*, and *Rabbits* are the chief zoological factors influencing ragwort in this country. The three former are controlling agents, while the action of rabbits in breaking the vegetation cover and exposing the soil, is, in general, distinctly favourable to the increase of the plant.

Owing to the absence of the European insect enemies of ragwort in New Zealand, they are of particular interest from an economic standpoint.

6. Over sixty insects, from five different orders, are recorded from ragwort, and a list of these, with notes on their life histories and alternative hosts, is made.

7. Two insects, the Arctiid moth, *Tyria jacobaeae* L. (cinnabar), and the Anthomyiid seed-fly, *Pegohylemyia seneciella* Meade, because of their extensive damage to the plant and their specific habits, are selected for special study. A number of other insects which cause a small amount of damage, also receive some attention.

8. Details of the life history of *Tyria* are worked out.

9. An account of the parasites reared from the larvae and pupae of *Tyria*, and their percentage infestation is given. This is the first rearing record of *Ichneumon perscrutator* Wsm., a parasite of the pupa.

10. Several fungi, which cause a mortality of 16–20 per cent. in *Tyria* pupae, were cultured and identified.

11. The mortality in the pupae of the cinnabar, due to the action of predators is found to be very high—about 60 per cent. Evidence points to the mole as the chief culprit.

12. An account is given of the life history, synonymy, and parasites of *Pegohylemyia seneciella* Meade. The mouth-parts and spiracles of the larva are figured.

13. The following species of insects cause a small amount of damage to ragwort: *Agromyza aeneiventris* Flin. (dipterous stem-borer), *Homeosoma nimbella* Dup. (lepidopterous stem-borer), *Phytomyza atricornis* Mg., and *Spilographa zoe* Loew. (leaf-miners), *Sphenella marginata* Flin. (flower-head fly), and *Aphis jacobaeae* Schr. A short account of the damage caused by these and the parasites reared from some of them is given.

14. A census of the ragwort and *Tyria* populations is made in several areas, and the methods employed described. Notes are made on the very extensive damage caused to the weed by the larvae of *Tyria*.

15. It is found that ragwort reacts to insect attack by producing a secondary crop of flowers and seeds. This reaction reduces the effectiveness of controlling insects. The whole of this aspect of the problem, showing how weed control by insects is more difficult of attainment than insect control by means of their entomophagous enemies is discussed.

16. Extensive experiments on the effect of cutting the whole plant or different parts of the plant, to simulate insect attack, were carried out. The following conclusions confirmed by observations on actual insect attack were reached:

(a) A badly attacked plant, if originally vigorous and if the growing season is good, has enough reserve energy to produce a second crop of seeds equal to 34.7 per cent. of the original potential yield producible in the absence of attack, thus reducing a total loss of 100 per cent. to one of 65.3 per cent.

(b) Plants with little or no reserve energy, growing on very poor soil, when badly attacked, do not produce seeds secondarily.

(c) Many plants which are unable to produce a second crop of flowers and seeds in the year of attack, may send out small shoots from the base of the stem. These shoots grow vigorously in the following year and are often capable of producing more seed than the original plant. Field observations show that this method of secondary growth has the effect of prolonging the life of the plant beyond the ordinary biennial period.

(d) Damage to any part of the plant (leaves, stem and flowers) will lower the seed yield for that season.

17. It is shown that *Tyria*, under certain conditions and in certain areas, has a controlling effect on ragwort in Britain, but in a wide, sandy area, like the Breckland of Norfolk, on account of its distribution not being uniformly general, it is less effective.

18. *Pegohylemyia seneciella*, in the south of England, infests 8-9 per cent. of the capitula of ragwort, and each larva destroys 75 per cent. of the seeds in the capitulum which it occupies. In the North of Scotland it is much more effective, 33-34 per cent. of the capitula being attacked.

19. The areas in England where some degree of control has been effected, are described for the purpose of comparison with conditions prevailing in the ragwort areas of New Zealand. The importance of eliminating factors, such as rabbit activity and overgrazing by farm animals, which predispose to open soil conditions, is strongly emphasised.

20. Indications of the future progress of the work are given, but it is too early yet to foretell the ultimate results of the researches.

21. Other methods of control—cultural, grazing, and chemical are described.

22. Details of collecting and shipping the controlling insects are given. In all 633,289 individuals were exported to New Zealand.

23. An extensive bibliography on weed control is appended.

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A QUANTITATIVE STUDY OF THE INFLUENCE OF TIDE UPON POPULATIONS OF *SALICORNIA EUROPEA*

By P. O. WIEHE.

(From the Department of Botany, Imperial College of
Science and Technology, London.)

(With Plate XXII and six Figures in the Text.)

I. INTRODUCTION.

THE salt marshes of the Dovey Estuary have been studied in some detail by Yapp, Jones, and Johns, and more recently by Richards. Yapp and Johns (5) have described the succession as taking place from a pioneer associes of *Salicornia europea* to one of *Juncus maritimus*, the progress of the succession being determined by the rate of accretion of soil on the marsh. The authors divide the succession into five zones, dominated by the following plants:

- (1) *Salicornia europea*, colonising mud flats.
- (2) *Glyceria maritima*, the dominant plant in the first sward on the marsh.
- (3) *Armeria maritima*.
- (4) *Festuca rubra*, the dominant species in the sward which follows the *Armeria* stage of the succession.
- (5) *Juncus maritimus*.

The work of these authors and of Richards (2) was concerned chiefly with the history of the succession from the *Glyceria* to the *Juncus* stages, and with the rate of accretion of soil during the succession through these stages. The present paper deals with the populations of *Salicornia europea* which colonise the mud flats.

The investigation was carried out at the Ynyslas end of the salt marshes (4), on the eastern side of the river Leri. In this region there is a pure stand of *Salicornia europea*, extending some 1500 ft. from the *Glyceria* sward toward the estuary. In the sketch map in Fig. 1 the upper limits of the neap and spring tides in this district are shown. Populations of *Salicornia* north of the neap-tide zone are submerged every 12 hours. Within the spring-tide zone the populations are submerged less frequently, the number of days in each lunar cycle free from tides varying from none at the northern limit of the zone to 15 days at the southern, landward limit. It is the specific purpose of this investigation to examine the relation between the density and vigour of *Salicornia*, and the frequency of submergence by the tide.

Five transects were chosen, running north and south, from the upper limit of the *Salicornia* associes to well within the neap-tide zone. Of these five

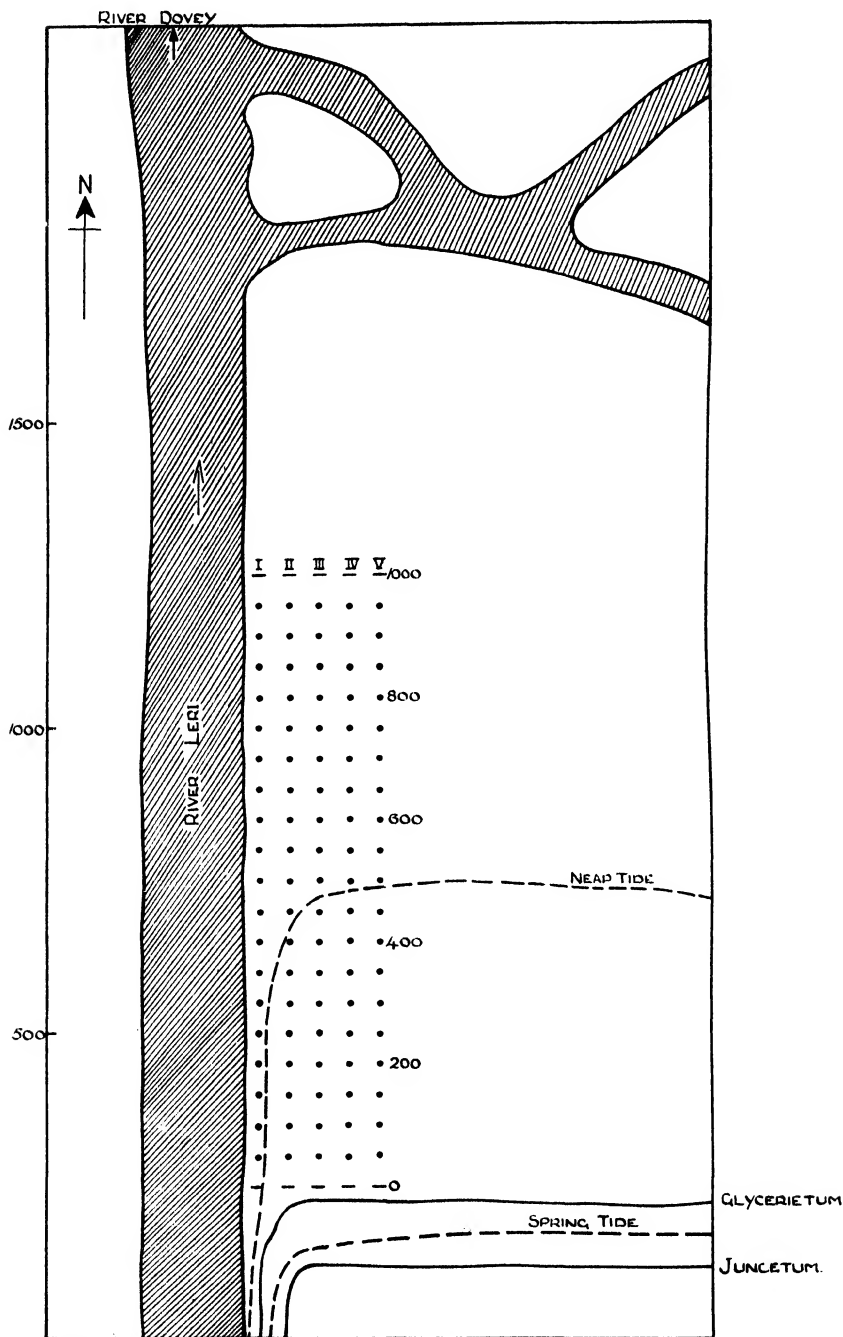


FIG. 1. Sketch map of the Ynyslas end of the Dovey Estuary, showing the upper limits of the neap- and spring-tides, the approximate boundaries of associates, and the position of the transects discussed in the text.

transects it will be seen in Fig. 1 that No. I lies entirely within the neap-tide zone, owing to the effect of the river on the tide level, and Nos. II-V lie across the tide zones. Every 50 ft. along transects I, III, IV, and V, at the points marked on the map, the number of individuals in 8 sq. ft. quadrats was recorded. The records were made in July 1934. In addition, at every alternate point on the map, i.e. every 100 ft. along each transect, five samples of ten plants each were taken at random, cut off at ground level, dried between blotting paper, and weighed on a portable balance.

Along transect II the data were collected somewhat differently. Counts of the number of individuals in 4 sq. ft. quadrats were made every 25 ft. along the transect, in April and again in July, in order to ascertain the mortality of seedlings during the intervening period. At points 300 and 800 ft. along transect II charts of quadrats were prepared showing the exact positions of plants in April and in July. Finally at five points along transect II (0, 250, 500, 750, and 1000 ft.) plants were dug up in July at random, and drawn to scale. Drawings were made of two specimen plants from each position, taken at random from the samples, and these are reproduced in Fig. 6. Transect II was sampled for wet weights in the same manner as the other transects.

The data include, therefore: (i) the density of individuals from five transects each 1000 ft. in length; (ii) the wet weight of individuals along these five transects; (iii) the density of individuals every 25 ft. along one transect in April and again in July; (iv) the exact position of individuals in two quadrats, 1 ft. sq., in April and July; and (v) scale drawings showing the morphology of individuals selected at random along one transect in July.

II. PRESENTATION OF DATA.

(i) *Density.* The densities of *Salicornia* along transects I-V are set out in Table I. Each figure is a mean of eight readings, except those along transect II, which are the means of four readings.

The population along the whole of transect I is subjected to daily submergence by the tide, and can so be used as a "control" in comparison with the data from transects II-V. The mean values for density in transects II-V are plotted in Fig. 2. It is clear that there is an increase in the density of *Salicornia* with increase in the periods between successive submergence by the tide, and that in transect I, all of which is within the neap-tide zone, there is no change in density along the transect. The trend of the data is obvious and needs no statistical demonstration.

(ii) *Wet weight.* The data obtained for the weight of ten plants from eleven plots on transects I-V are set out in Table II.

There is some indication that the plants in the neap-tide zone, where the density is lowest, are heavier. The data have been analysed by Fisher's method of separating the variances (1), and the results of the analysis are set out in Table III. For the purposes of the analysis the values at 500 ft., on the upper

Table I. *Density of Salicornia europaea in number of individuals per square foot, along five transects described from Fig. 1.*

Distance in ft.	Transect					Mean for Nos. II-V
	I	II	III	IV	V	
0	3	30	25	32	22	27.5
50	2	61	37	64	57	54.0
100	1	47	93	74	76	72.5
150	1	35	46	62	62	51.0
200	3	84	51	60	47	58.5
250	5	59	88	62	65	66.0
300	2	58	81	49	38	56.5
350	2	60	95	30	10	48.7
400	1	53	53	17	23	36.0
450	2	60	40	48	41	47.0
500	3	24	28	8	13	18.0
550	3	16	16	9	7	12.0
600	4	13	7	17	19	14.0
650	2	13	10	15	15	13.0
700	4	8	9	12	12	10.0
750	1	6	8	7	12	8.0
800	1	8	5	7	8	7.0
850	2	6	3	9	3	5.0
900	2	4	5	4	2	4.0
950	3	2	3	1	3	2.0
1000	2	1	1	1	1	1.0
Total	49	648	704	588	536	

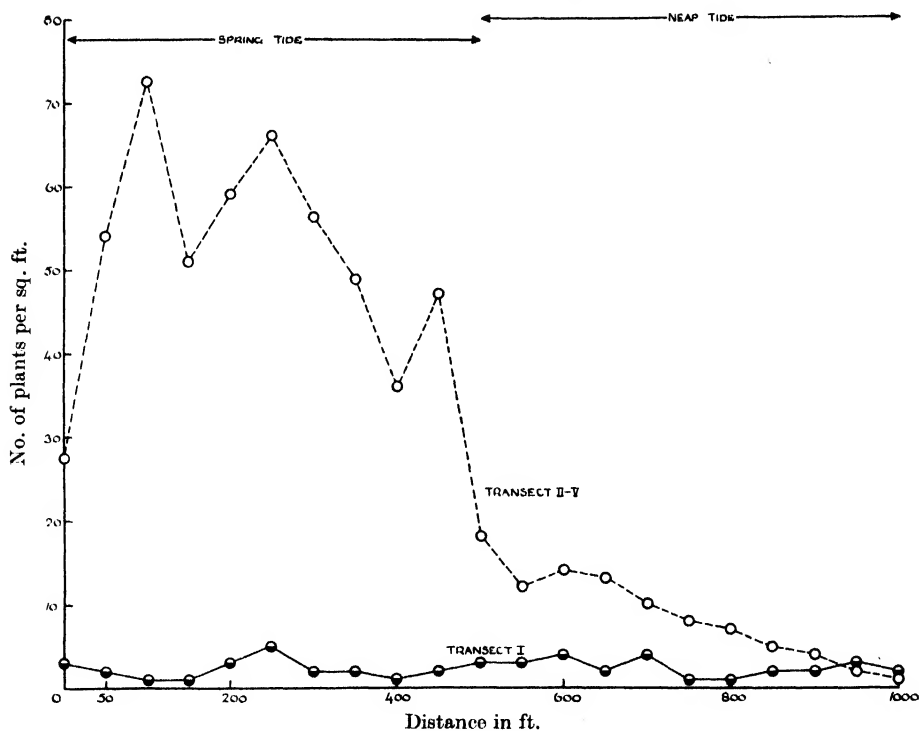


FIG. 2. Mean density of *Salicornia* expressed as plants per square foot, plotted against distance along transect. Values along the dotted line are the means of transects II to V; those along the continuous line are the means along transect I.

Table II. *Wet weight of ten plants of Salicornia europea, in grams, from eleven positions along transects I-V. Each value is the mean of five weighings.*

Distance in ft.	Transect					Mean for Nos. 11-V	Mean
	I	II	III	IV	V		
0	9.00	5.42	7.74	4.32	4.86	6.44	5.99
100	9.72	6.48	4.50	3.60	4.32	4.72	
200	8.64	8.46	6.48	5.76	4.86	6.39	
300	11.52	5.76	6.48	8.10	7.56	6.97	
400	9.36	6.84	5.04	4.50	5.40	5.44	
500	8.28	7.20	7.20	5.94	6.66	6.75	8.88
600	9.90	4.86	5.94	9.10	5.64	6.62	
700	11.60	9.36	9.90	13.50	9.18	10.48	
800	7.56	6.30	8.82	5.76	5.58	6.61	
900	11.16	7.20	8.46	9.00	9.18	8.46	
1000	10.80	11.12	12.60	11.70	13.50	12.23	
Total	107.54	79.00	83.16	81.28	76.74		

Table III.

Variance due to	Degrees of freedom	Sums of squares	Variance	z	1 % point	5 % point
Transect	3	6.817	2.272	1.572	1.631	1.071
Samples within spring-tide zone	4	7.153	1.789	1.453	1.300	0.864
Samples within neap-tide zone	4	50.361	12.589	2.430	1.300	0.864
Between neap- and spring tide zones	1	38.761	38.761	2.990	4.379	2.769
Interaction of transect and position in transect	27	120.893	4.477	1.912	0.370	0.257
Error	160	15.685	0.098			
Total	199	239.669				

limit of the neap-tide zone, have been omitted, in order to obtain a symmetrical table.

From an inspection of Table III it will be seen that the variance due to transect is insignificant on the 1 per cent. points; so also is the variance due to differences between the neap- and spring-tide zones. It may be concluded, therefore, that although there are fewer individuals per unit area within the neap-tide zone, those individuals are as big as (or, on the criterion of the 5 per cent. points, bigger than) the individuals in the spring-tide zone.

The significant variance *within* the two tide zones is due to the presence of scattered pans in the salt marsh. The larger variance within the neap-tide zone is probably due to the fact that samples are more scattered in this area, and sampling is less accurate on that account. That the pans, where the vigour of *Salicornia* is higher, do not lie regularly across the transects, but are scattered irregularly, is indicated by the highly significant interaction variance, which shows that the effect of position along a transect varies in different transects.

(iii) *Mortality of seedlings.* Along transect II data for the density of individuals were collected in April and from the same quadrats in July. From these values the percentage mortality in relation to tide level can be found. The data are given in Table IV, and a mortality curve constructed from the last column of Table IV is to be found in Fig. 3.

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Table IV. *Density of Salicornia europaea from plots of 4 sq. ft., in April and July. Data taken every 25 ft. along transect II, and given in individuals per square foot. The values for percentage mortality are calculated from the two columns of density values (= M per cent.).*

Distance in ft.	Seedlings in April	Adults in July	M %	Distance in ft.	Seedlings in April	Adults in July	M %
50	56	37	33.9	525	56	9	83.9
75	76	54	26.7	550	52	16	69.2
100	135	93	31.1	600	47	7	85.1
125	64	54	15.6	625	25	7	72.0
150	64	46	28.1	650	37	10	73.0
175	110	71	35.4	675	35	28	80.0
200	79	51	35.4	700	43	9	79.0
225	93	77	17.1	725	41	14	69.0
250	126	88	30.1	750	43	8	81.3
275	160	89	45.0	775	45	5	87.3
300	104	81	22.1	800	39	34	87.1
325	163	85	47.7	825	49	4	91.8
350	139	95	31.6	850	58	3	94.8
375	61	49	20.0	875	29	5	82.6
400	74	53	28.3	900	27	5	81.4
425	67	54	19.1	925	32	5	84.2
450	73	40	45.2	950	38	3	92.1
500	50	28	44.0	975	33	1	93.0
				1000	32	1	96.8

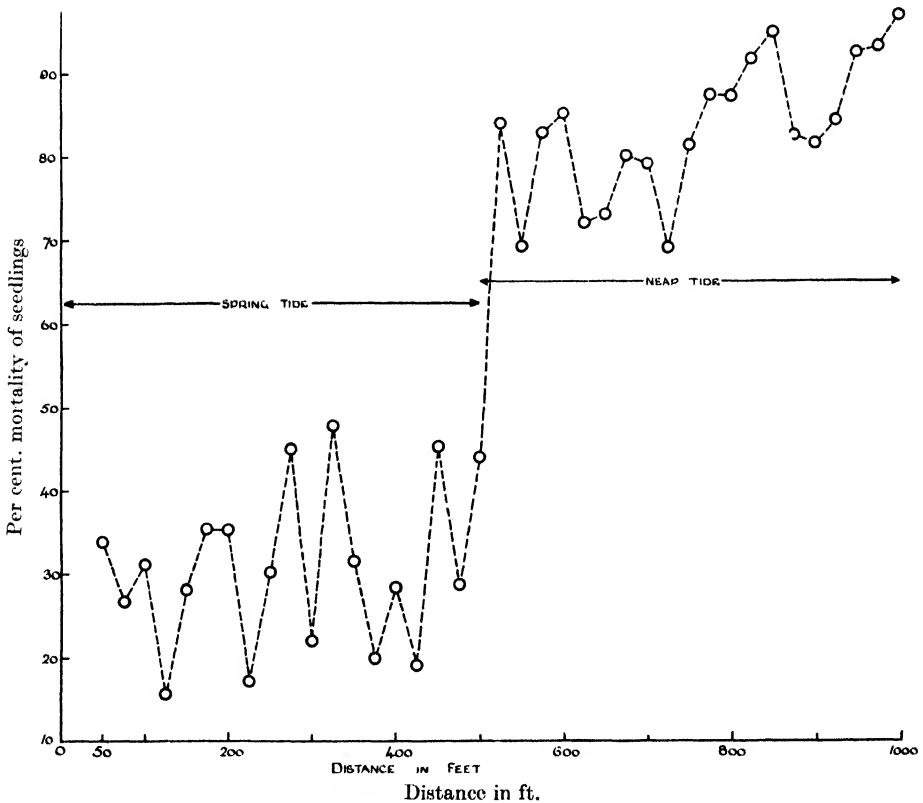


FIG. 3. Percentage mortality of *Salicornia* seedlings along transect II.

It will be seen from Fig. 3 that the percentage mortality is uniformly high in the neap-tide zone, and comparatively low in the spring-tide zone. The transition is sharp; there is no gradual decrease in percentage mortality corresponding to the increase in periods between successive inundations by the tide.

III. DISCUSSION.

The relation between density of adult *Salicornia* plants and the neap- and spring-tide levels is given in Fig. 2. Within the neap-tide zone the populations are submerged every 12 hours; within the spring-tide zone the populations are

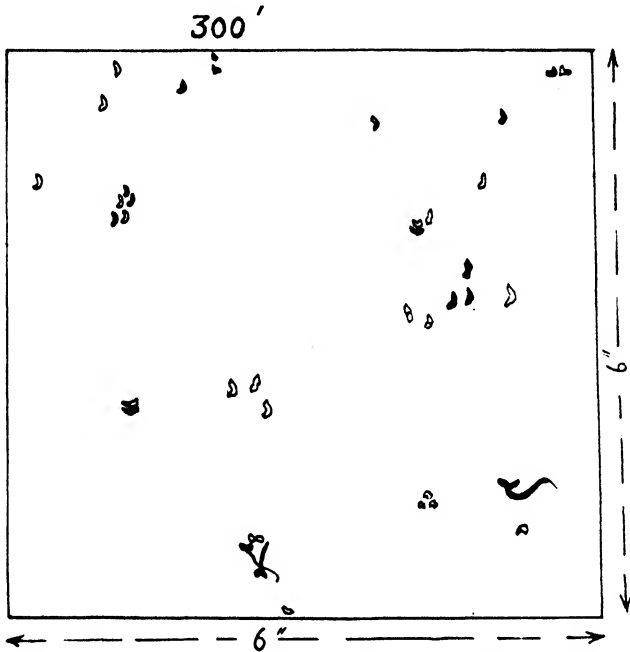


FIG. 4. Chart-quadrat showing positions of *Salicornia* seedlings in April, in the spring-tide zone. The individuals shown in black had died by July.

free from the effects of tides for periods varying from 1 day in 16 in the middle of the transect to 15 out of 16 days at the landward end of the transect. The falling off in density in the first 100 ft. of the transect is due to the colonisation of the *Salicornia* associates by *Glyceria*. It is clear from the figure that there is a high correlation between density of individuals and the number of days they are free from submergence by the tides. The appearance of sample plots at 200, 500 and 1000 ft. along transect II can be gathered from the photographs in Plate XXII (opposite p. 332).

The manner in which density is determined by frequency of submergence appears from inspection of Fig. 3, in which the percentage mortality is plotted against position along transect II. Within the neap-tide zone about 80 per cent.

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of the seedlings recorded in April have disappeared by July; within the spring-tide zone only 35 per cent. have disappeared. The transition in percentage mortality between the two zones is sharp, and does not follow the gradual increase in number of days between submergences, from the seaward toward the landward limits of the spring-tide zone. It seems clear from Fig. 3 that in populations submerged by the tide every 12 hours very few *Salicornia* seedlings are able to become established. If, however, there are occasional periods of 2 or 3 days during which the populations of seedlings are undisturbed by the tide, as many as 65 per cent. of the seedlings become established. There is a "threshold value" of time which the seedlings require

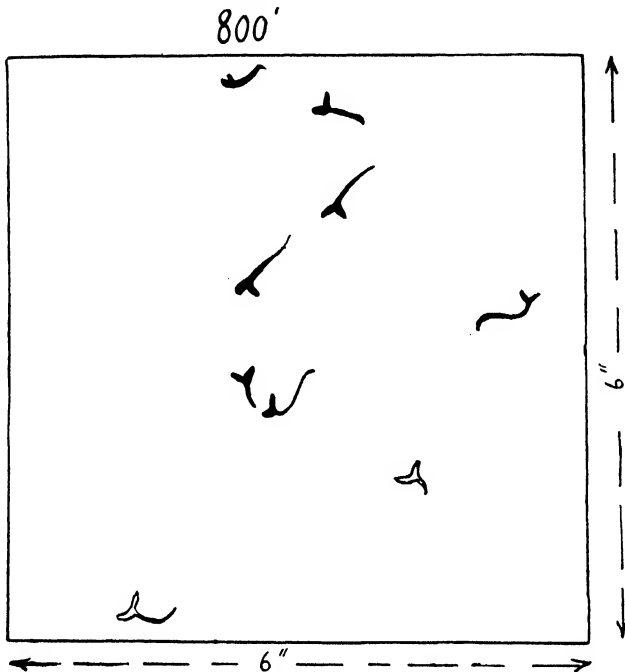


FIG. 5. Chart-quadrat showing positions of *Salicornia* seedlings in April, in the neap-tide zone. The individuals shown in black had died by July.

for their establishment. Periods between successive tides longer than this threshold value have no effect in reducing the mortality below an average of 35 per cent. Therefore, although the frequency of submergence by the tide decreases from the upper neap-tide limit to the upper spring-tide limit, there is no parallel decrease in the mortality of seedlings. Reference to Table IV shows that the density of individuals in July depends not only on the mortality, but also on the absolute number of seedlings present. There are many more seedlings initially present in the spring-tide zone than in the neap-tide zone.

The specific effect of inundation on the seedlings was studied by making chart-quadrats on which were marked the exact positions of plants in April

and in July. Two such charts, from positions 300 and 800 ft. along transect II, are reproduced in Figs. 4 and 5. The positions of all seedlings present in April were marked, and those which had died or disappeared by July were represented in black on the chart. In the chart taken at 300 ft., within the spring-tide zone, twelve out of a total of thirty-nine died. Of these twelve it can be seen that three had been dragged by the tide, so that their stems lay horizontally. In the chart taken at 800 ft., seven out of a total of nine

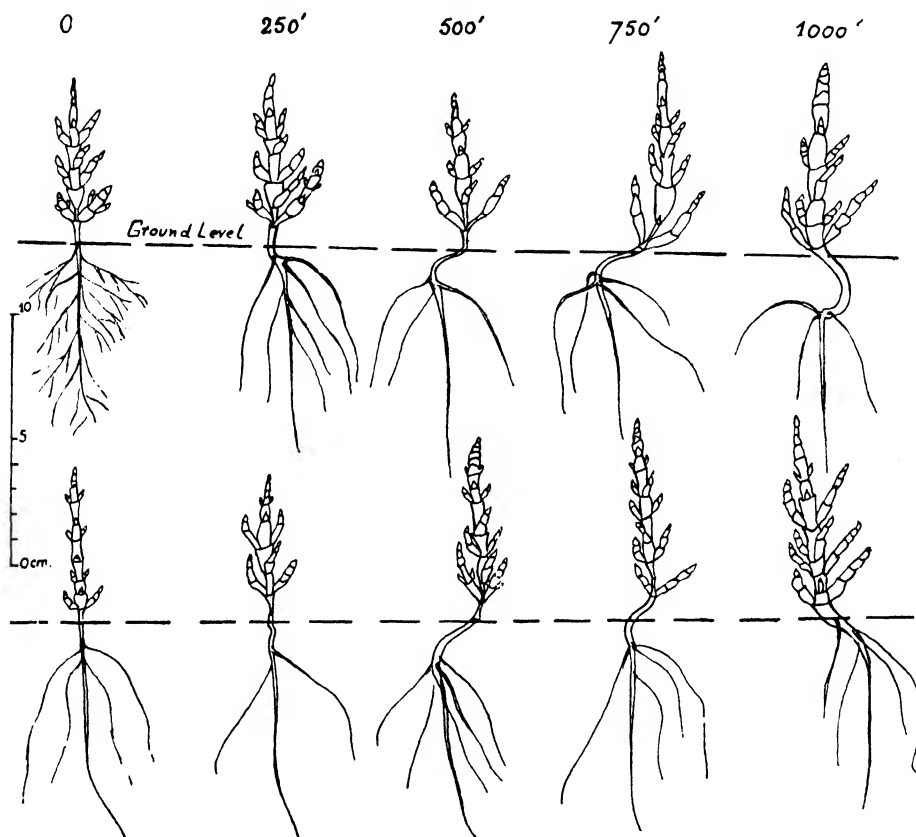


FIG. 6. Scale drawing showing morphology of *Salicornia* plants in July, taken at random from five positions along transect II.

plants died. All the dead plants had been dragged by the tide, and the two survivors showed signs of the same treatment.

In July adult plants, taken at random from five positions along transect II, were carefully dug up and drawn to scale. Their morphology is shown by the scale drawings in Fig. 6. *All the survivors in the neap-tide zone bear signs of early dragging by the tides*, to which they were subjected every 12 hours. Plants in the spring-tide zone, at 0 and 250 ft., show no sign of having been dragged by the tide.

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It may be concluded therefore that the density of *Salicornia* along the transects described depends upon (i) the number of seeds which germinate, and (ii) a threshold value of time, apparently not more than 2 or 3 days, during which the seedlings are undisturbed by tides, and which is necessary for their establishment.

From the analysis of the wet weight data in Table III it may be concluded that once a plant has become established, frequent submergence by the tide does not inhibit its growth. In fact the data indicate that the wet weights of plants are greater when the plants are submerged every 12 hours. Whether this increased wet weight is indicative of greater dry weight, or is merely due to greater succulence, cannot be deduced from the present data.

IV. SUMMARY.

1. An investigation was carried out at the Ynyslas end of the Dovey salt marshes in order to examine the relation between the density and vigour of populations of *Salicornia europaea* and frequency of submergence by tides.

2. Data for density of individuals and wet weight were collected from five transects, 1000 ft. in length; four lying across the spring- and neap-tide zones, and one lying entirely within the neap-tide zone. The densities along one transect were taken in April 1934, and again in July, from which information the percentage mortality of seedlings along this transect was calculated.

3. Within the neap-tide zone, where populations are submerged every 12 hours, only 25 per cent. of the seedlings survive. In the spring-tide zone, across which the periods between successive tides vary from 1 to 15 days, about 65 per cent. of the seedlings survive.

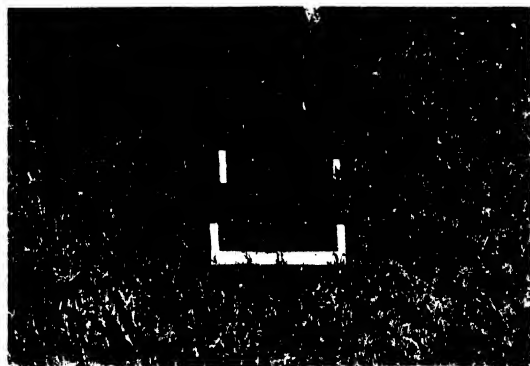
4. From these data it is concluded that a "threshold" time of about 2 or 3 days undisturbed by tides, is necessary for the establishment of a dense population of *Salicornia*. Longer periods between successive tides do not reduce the mortality of the seedlings.

5. From a comparison of chart-quadrats taken in April and July, and from an inspection of the morphology of the surviving plants, it is seen that the daily tides act deleteriously by dragging the seedlings from their anchorage in the mud.

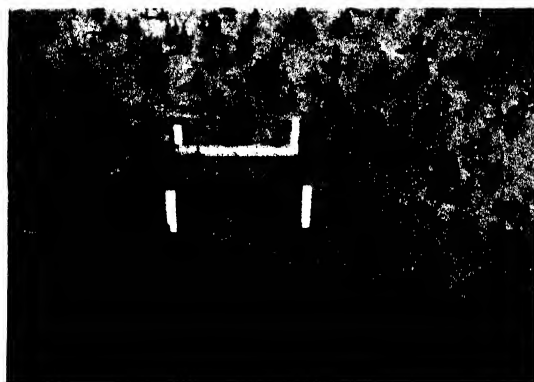
6. The number of germinating seeds of *Salicornia* is greater in the spring-tide zone than in the neap-tide zone.

7. From the data for wet weights it is concluded that once a plant has become established, daily submergence by the tide does not inhibit its growth.

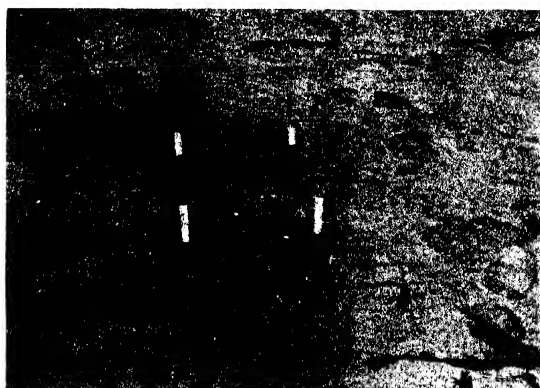
The author has pleasure in recording his thanks to Mr William Davies for facilities granted at the Welsh Plant Breeding Station, and to Dr Eric Ashby, for his help in the preparation of this paper.



Phot. 1.



Phot. 2.



Phot. 3.

Photographs taken at distances 200, 500 and 1000 feet along transect II, illustrating the difference in density of *Salicornia* at different levels of the tidal zone. The pegs enclose an area of 1 sq. foot.

WIEHE—QUANTITATIVE STUDY OF THE INFLUENCE OF TIDE UPON
POPULATIONS OF *SALICORNIA*

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CERTAIN ENVIRONMENTAL FACTORS OF A SAND BEACH IN THE ST ANDREWS REGION, NEW BRUNSWICK, WITH A PRELIMINARY DESIGNATION OF THE INTER- TIDAL COMMUNITIES.

By CURTIS L. NEWCOMBE.

(*The Atlantic Biological Station and The Johns Hopkins University.*)

(*With two Figures in the Text.*)

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INTRODUCTION.

THIS paper is offered as a contribution to the knowledge of intertidal communities and of factors operating in the sand beach that influence the organisms present.

Personal observations at widely separated localities on the Pacific as well as the Atlantic coast have resulted in the recognition of certain general dominants which are extensive in range and, in the light of our present

knowledge, appear most suitable for naming the intertidal communities. The relationship between plants and animals on land is known to be very different from that in the sea. Clements and Shelford (1927) say that: "On land, plants are the universal dominants, though not to the entire exclusion of the animals, while in the ocean and in all major water bodies, animals constitute the dominants and plants are secondary." Intertidal animals do dominate, but there are certain algae, such as *Fucus vesiculosus* and *Ascophyllum nodosum*, to which co-dominant rank must be accorded. The basis employed for evaluating the members of a major community should be stated. In many studies of biotic communities, quantitative methods have not developed to the extent of rendering possible a thorough statistical treatment of the data. Clearly, before the analysis of quantitative results can be undertaken, the probable errors involved in the actual experiments must be reduced to insignificance. Due to the absence of methods possessing this degree of precision, there is a decided need for a maximum number of counts and observations possible under existing conditions. Another obstacle is the lack of knowledge pertaining to ecological relations of many common littoral organisms. Notwithstanding these facts, some authors, notably Towler (1930), have courageously attempted the task of classifying various members of certain marine communities on a basis of their degree of influence on the other members of the community and their control of the habitat.

The naming of marine communities on a basis of their characteristic organisms, introduced by Petersen (1915), is, unquestionably, a very satisfactory means for studying distribution and interrelationships of animals in and on the sea bottom. Faunal surveys on the Atlantic coast of America have yielded some very useful information about the kind and distribution of animal life (Verrill, 1873; Sumner, Osburn and Cole, 1913). The absence in many instances of any expression of quantity is regrettable, and lessens the value of the work for solving some important biological problems. In this paper, the community nomenclature of Shelford (private communication) and his associates has been used with a few modifications. For the reader's convenience, the terms are defined here.

Dominants control the habitat biota, being of outstanding abundance or conspicuous influence in the community throughout the entire active or growing season. On land they are usually plants, whereas in salt and fresh water, animals most often dominate.

Co-dominants are dominant plants occurring among several dominant animals and present during the entire growing season.

Subdominants have important influence in the control of the life of the habitat, but are usually present only during a part of the active or growing season.

Influents are common forms which have important relations in the biotic balance and in the community. They affect (*a*) the bodily well-being of certain

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sessile forms, such as *Fucus* and *Ascophyllum*, by predatorial action, or (b) the numbers of associated organisms without altering the essential composition of the biotic community or markedly changing the rate of succession, or (c) the abundance of food.

Subinfluents exert a lesser influence. Normally they are present during only a part of the year.

Secondary forms are considered to be those of minor influence in the community. They usually occupy a narrow range or a local habitat and occur in relatively small numbers.

A *biotic community* is an assemblage of relatively uniform taxonomic composition and physiognomy.

A *habitat* is an area occupied by a community, the life of which is controlled by climate, soil, substratum or water. There are two types of habitats recognizable: (1) the major habitats such as grassland or deciduous forest on land and sand or rock habitats on the seashore, all of which are extensive; (2) the local habitats, determined by soil, water, or illumination, and usually occurring locally in the major habitats and constituting breaks within them.

The practice adopted by the writer has been to name the communities after the *dominants*, primarily stressing abundance and uniformity of distribution and degree of influence as far as existing information will permit. The major communities are briefly described in Part I and an account of certain physical factors operating on a sand beach of the St Andrews (New Brunswick) region is presented in Part II.

PART I. INTERTIDAL COMMUNITIES WITH SPECIAL REFERENCE TO THOSE OF THE SAND BEACH.

During recent years, biologists have shown a greater interest in the study of biotic communities. The intimate relationships of animals and plants have been studied by Shelford (1913), Weese (1924), Blake (1926), King (1927), Johnson and Skutch (1928), Smith (1928), Shackleford (1929), and Bird (1930) in North America; Cameron (1917) and Watt (1923) in Europe; Oliver (1923) working on the intertidal communities of New Zealand; and Phillips (1931) who has investigated certain inland communities of South Africa.

Shelford (1930), in naming marine biotic communities, uses "*Balanus-Littorina* Biome" for the biotic intertidal community of wide extent, probably ranging from central Alaska to San Diego, California. Thus, the generic names of the dominants of the epifauna are employed for designation of the major communities. That a comparable major community exists in the intertidal region at St Andrews there can be no doubt. Furthermore, from the literature, it appears quite likely that this biome has a very extensive distribution along the coasts of the United States and Canada.

On the basis of a study of intertidal communities around San Juan Island, Washington, and also in the Bay of Fundy region, recognition of two biomes

living mixed together in the intertidal belt is justifiable. These may be tentatively named the "*Balanus-Littorina-Fucus* biome" and the "*Mya-Nereis virens* biome". The animals of the "*Balanus-Littorina-Fucus* biome" are what Petersen called epifauna, often loosely referred to as onfauna. Those of the "*Mya-Nereis virens* biome" constitute the subterranean community, living in the bottom materials and known as infauna. Hence, there are two biomes living mixed together, the sand community of the intertidal belt corresponding to grassland and the rock community to forest in a parkland. Obviously, the physiognomy, more characteristic life forms, and all the demands of the members of the community are different in the two.

There is given below a brief description of the major communities of the St Andrews region and a more detailed treatment of the physiography and biota of the sand beach.

A. METHODS.

Random sampling was the method employed in this study, supplemented by cruising. In the case of the smaller and more uniformly distributed animals, records of abundance were obtained per two decimetre square area and later computed to the number per metre square area at the various stations. Three permanent quadrats, A1, A2, and A3 of transect A, each about 10 sq. m. in area, were selected at the desired levels of the intertidal zone for intensive study. In the case of larger and less uniformly distributed forms, such as clams and worms, metre square areas were examined at a depth sufficient to include all the desired organisms.

B. DESCRIPTION OF SAND BEACH.

The sand beach studied (transect A) is located near the mouth of the St Croix River, New Brunswick, and has a uniform but fairly steep slope. The distance between mean low-water level and mean high-water level is approximately 65 m. and the tidal amplitude about 6 m. (20 ft.). Other beaches of this region exhibit a much more gradual slope, for example, Clam Cove, where the distance between the high- and low-water levels is over 400 m. Below the mean low-water level, the beach has a very gradual slope, the distance to the low-water level of spring tides being about 30 m. In general, the grade of soil becomes fine in an offshore direction, some mud occurring near the mean low-water level, whereas the area exposed only during spring tides possesses a very high percentage of soft mud. Here, the sulphide content is above average, figures as high as 45 volumes per cent. being frequently obtained. For a distance of 12 m. below the mean high-water level, the soil consists of coarse sand covered with a regular surface of small stones, the most numerous ones being from 25 to 80 mm. in maximum diameter. The area below this zone, to the mean low-water level, is characterised by a finer grade of sand. Large stones, 30 cm. or more in diameter, are sparsely scattered over the

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beach, affording a shelter for animals (for example, species of *Littorina* and *Gammarus*) and a surface for the attachment of barnacles as well as different algae, such as *Fucus* and *Ascophyllum*.

The quadrats selected for intensive study are designated A1—about 5.5 m. (18 ft.) above chart datum and approximately 50 m. from the mean low-water level in a shoreward direction; A2—located about 13 ft. above chart datum and 24 m. from the mean low-water level; and A3—about 7 ft. above chart datum and 11 m. from the mean low-water level (see p. 334).

C. DESCRIPTION OF COMMUNITIES OF SAND BEACH.

On account of this somewhat mixed type of habitat, two major communities are represented, namely, the *Balanus-Littorina-Fucus* biome corresponding to the *Picea-Alces* biome, and the *Mya-Nereis virens* biome analogous to the *Stipa-Bison bison* biome. These two major intertidal communities correspond to Petersen's "epifauna" and "infauna". They constitute distinct and separate biomes living together over part of their range and hence are similar to savannah.

(1) *The Balanus-Littorina-Fucus biome.*

The dominants of this biotic community are *Balanus balanoides*, *Littorina litorea* and *Fucus vesiculosus*. From records in the literature of collections made at widely separated points, it seems that this major community is of wide extent, ranging at least from the coast of Newfoundland to New York State. The number of associations of the biome is not known. In the Gulf of Maine, the *Balanus-Mytilus edulis* association is recognised (Newcombe, 1935). The composition of this biome is shown below.

Dominants: *Balanus balanoides*, *Littorina litorea*.

Co-dominants: *Fucus vesiculosus*, *Ascophyllum nodosum*.

Subdominants: *Mytilus edulis*, *Littorina rudis*.

Influents: *Purpura lapillus*, *Littorina palliata*.

Subinfluents: *Lunatia heros*, *Acmaea testudinalis*, *Gammarus marinus*.

Secondary animals: *Sertularia* sp. and other hydroids, *Metridium dianthus*, *Bugula murrayana*, *Asterias vulgaris*, *Asterias forbesii*, *Tonicella marmorea*, *Buccinum undatum*.

The position in the community of some of the secondary forms is difficult to evaluate. Often they occur in clans and their distribution is irregular and seasonal. Some echinoderms are seasonal invaders from below the mean low-water level. In this connection, there should be mentioned *Asterias vulgaris*, *A. forbesii* and *Strongylocentrotus drobachiensis*, which are probably dominants of the major subtidal community of this region (compare Shelford and Towler, 1925, p. 59). They cannot be said to exert an important influence on the entire community, but they are a distinct limiting factor as far as the downward distribution of the biome is concerned. This limiting influence is effective on

practically all types of substratum in the St Andrews region, namely, rock, gravel, mud and wharf pilings (Newcombe, 1935).

Certain abundant forms, such as *Balanus* and *Littorina*, occur together as a rule and in cases make similar demands on the habitat, yet their seasonal influence on the physiognomy of the community is quite different. For example, during 1931 the set of barnacles at St Andrews occurred chiefly in May. Consequently, throughout June the exposed rock surfaces of the intertidal zone were literally covered with small barnacles ranging up to 3 or 4 mm. in height and frequently numbering as high as 2500 per sq. dem. (Table I). The physiognomy in September differed markedly from that of June, due not only to destruction by predators, which include *Purpura lapillus* and *Littorina litorea*, but also to the removal of barnacles and variations in their shape due to crowding. Another factor in producing a pronounced change in the appearance of the entire biome is the limiting effect of illumination on growth rate during the summer period in areas directly exposed (Klugh and Newcombe, 1932). The change in the barnacle population during the winter season is usually slight, local disturbances being caused by ice. The reduction during the winter of 1930-1 was pronounced (Table I).

Table I. *Abundance of more important members of the Balanus-Littorina-Fucus biome during the summer and winter seasons of 1930-1 at St Andrews, New Brunswick.*

Quadrat A1 (level 18 ft. above chart datum).				
Species	Date	No. per sq. m.	Average size	
			Length mm.	Width mm.
<i>Balanus balanoides</i>	Aug. 20-25, 1930	3000-5000	2-5	4-7
	Feb. 24-29, 1931	1500-3000	2-6	4-8
<i>Littorina rudis</i>	Aug. 20-25, 1930	700-900	14	9
	Feb. 24-29, 1931	3000-5000	5	4
<i>L. litorea</i>	Aug. 20-25, 1930	50-70	11	11
<i>Mytilus edulis</i>	Aug. 20-25, 1930	30-40	14	9
	Feb. 24-29, 1931	30-40	15	10
<i>Purpura lapillus</i>	Aug. 20-25, 1930	20-40	25	15
Quadrat A3 (level 7 ft. above chart datum).				
<i>Balanus balanoides</i>	Aug. 20-25, 1930	4000-5000	5	7
	Feb. 24-29, 1931	Sparse	—	—
<i>Mytilus edulis</i>	Aug. 20-25, 1930	1600-2000	11	—
	Feb. 24-29, 1931	5000-8000	8	—
<i>Littorina littorea</i>	Aug. 20-25, 1930	300-500	11	—
	Feb. 24-29, 1931	700-800	—	—
<i>Acmaea testudinalis</i>	Aug. 20-25, 1930	100-300	10	—
<i>Littorina rudis</i>	Aug. 20-25, 1930	100-200	5	4
<i>Purpura lapillus</i>	Aug. 20-25, 1930	70-100	27	17

There occur three species of *Littorina* (*L. rudis*, *L. litorea* and *L. palliata*), whose differing resistance to unfavourable conditions is reflected in their range of vertical distribution, as is clearly shown by Gowenlock and Hayes (1926). These widely distributed gastropods are, like barnacles, present throughout all seasons, and hence *Littorina litorea* and *L. rudis* have been accorded the

rank of dominants in the major community. During the winter season, they are not regularly distributed as they are throughout almost the whole of the rest of the year. Some move down the beach to a lower and hence less exposed level. All seek shelter under algae, rocks or in tidepools, where they may be found in very large numbers.

Mytilus edulis are most abundant at the lower levels, sometimes occurring as irregularly scattered clans. In transect A they are fairly evenly distributed at the lower levels and become less regular at the upper limits of their vertical range where the growth rate is slower, as shown by the annual rings on the valves (Mossop, 1922). Their lower range is abruptly terminated by the predatorial seasonal influence of sea urchins, *Strongylocentrotus drobachiensis*, and starfishes, *Asterias vulgaris* and *A. forbesii*, of the *Strongylocentrotus-Asterias* biome (Newcombe, 1935). This interaction between members of the two biomes is of wide extent in the St Andrews region, being most apparent in the wharf-piling communities. A general picture of the relative abundance of the several influents of this biome during the summer and winter seasons is presented in Table I. Members of the genus *Gammarus* occur in large numbers across the intertidal zone during all seasons. Throughout the winter period they are most abundant in protected places and their relative abundance is greater at the lower levels. The three species present are *Gammarus annulatus*, *G. marinus* and *G. locusta* (Pentland, 1933).

Fucus vesiculosus and *Ascophyllum nodosum* are quite regularly distributed between the half-tide level and the mean low-water level and are represented by scattered individual plants at the higher levels. These algae constitute an important source of food as well as protection for several gastropods during extreme climatic conditions. Among scattered algae¹ occurring at the lower levels in this locality may be mentioned

Enteromorpha linza
E. erecta (?)
Illea fascia
Rhizoclonium tortuosum
Ectocarpus confervoides
E. tomentosus
E. siliculosus
Scytosiphon lomentarius
Chorda filum

Desmarestia viridis
Fucus platycarpus
Porphyra umbilicalis
P. laciniata
Chondrus crispus
Polysiphonia fastigiata
P. Scheubleri (?)
P. urceolata

(2) *The Mya-Nereis virens biome.*

In the Bay of Fundy region, the *Mya-Nereis virens* biome is of wide extent in the intertidal zone. In general, its dominants decrease in numbers toward the upper levels. Below the mean low-water mark *Mya arenaria* is only occasionally found, and submerged *Mya* communities are not known to occur.

¹ Acknowledgment is made to the late Prof. A. Brooker Klugh, and to Dr William Randolph Taylor for the identification of marine algae.

It has been demonstrated experimentally that the general limitation of the distribution of *Mya arenaria* below the mean low-water level in the Bay of Fundy region is due largely to two soil types: (a) fine shifting sand, and (b) soil consisting of a high percentage of mud with a surface layer of fine silt (Newcombe, 1936). In the Gulf of St Lawrence and the Chesapeake Bay, it has been observed that *Mya* communities occupy a subtidal position. Furthermore, Prof. Shelford states (private communication) that in the Baltic Sea a corresponding community extends several metres below the low-tide level, and that in the Puget Sound area it reaches from 1½ m. above low tide to 8 m. below the low-tide mark. Information is not available pertaining to the subtidal abundance and distribution of *Nereis virens*.

Natural forces operating locally toward the partial extermination of this infaunal biome are found in the *Balanus-Mytilus edulis* association. During favourable seasons for development of this association, surface conditions caused by the accumulation of shells, stones, or other materials in localised areas may permit heavy sets of mussels, which spread rapidly and form a surface layer that kills the clams and alters the physical and chemical conditions in the subsurface layers.

Little attention has been devoted to the secondary animals of this major infaunal community. The principal constituents are given here.

Dominants: *Mya arenaria*, *Nereis virens*.

Subdominants: *Cerebratulus marginatus*.

Influents: *Macoma baltica*.

Subinfluents: *Lineus ruber*, small annelid (not identified).

On the basis of available data, it appears that this biome is of wide extent in the Gulf of Maine, being the intertidal community of greatest economic value to the fisheries of the region. Furthermore, on account of its stability and location it is very suitable for analysis.

South of Cape Cod, Massachusetts, different associations exist, and the influence of *Venus mercenaria* becomes dominant south of New York State. Throughout the entire Bay of Fundy region, *Mya arenaria* and *Nereis virens* are dominant. The numbers of the former vary considerably, depending on the factors operating to limit survival of set and rate of growth. Under favourable conditions, a set numbering as high as 6000 per sq. m. has been obtained, whereas from 200 to 300 above 20 mm. in length per square metre may be considered typical for the region. Soil consisting of shifting sand or mud with a surface layer of silt has been demonstrated to be unfavourable for survival of set as well as for the growth of this lamellibranch (Newcombe, 1936).

In transect A, seasonal fluctuations in abundance of infauna were not pronounced. At the level of quadrat A1 near the upper limit of their distribution, the soft-shelled clams, *Mya arenaria*, were only occasionally present, numbering about four per square metre. At the level of quadrat A3, the

numbers were somewhat greater, namely thirty to forty per square metre, but still considerably less than the representative numbers for the region.

A comparison of the bivalve fauna of the subterranean biomes in the Bay of Fundy (Atlantic coast) and Puget Sound (Pacific coast) regions reveals several cogent points of interest. In the former area *Mya arenaria* is the

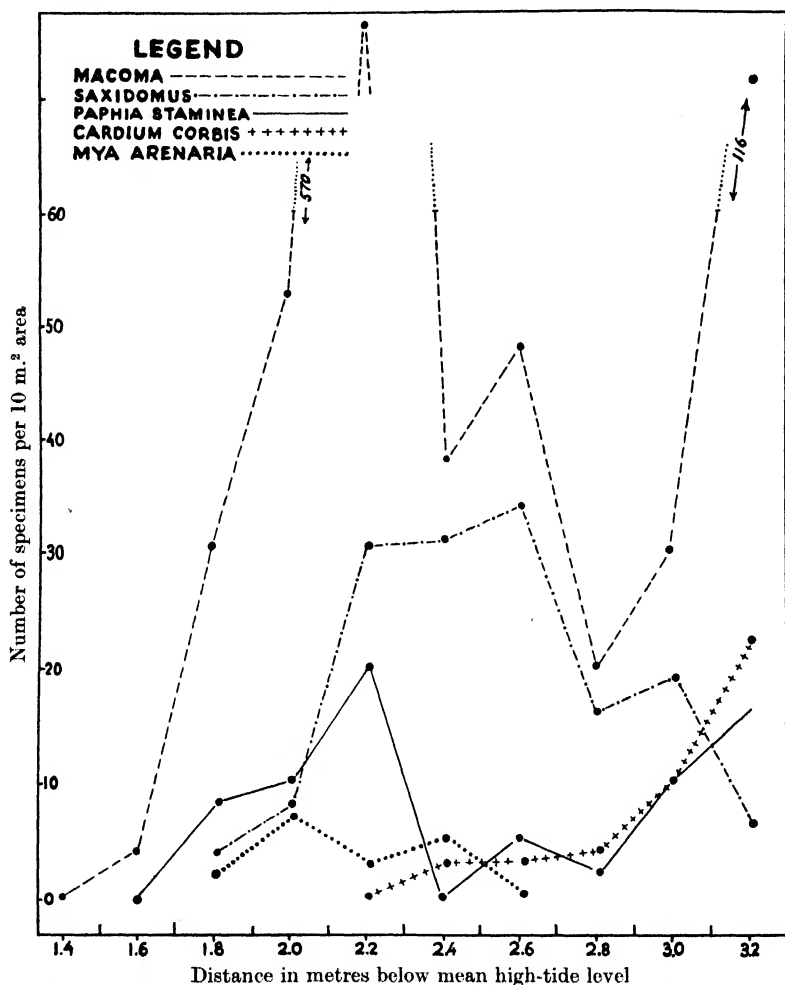


FIG. 1. Relative abundance of several Lamellibranchs of the intertidal zone at Flat Point near Friday Harbor, Washington.

dominant lamellibranch and *Macoma baltica* represents practically the only associated bivalve, numbers ranging from fifty to seventy per square metre area being commonly obtained. A study of the infaunal population of the beach at Flat Point near Friday Harbor, Washington (Puget Sound region), has revealed the presence of five important bivalves occupying the same habitat and occurring in maximum numbers at levels between 2.0 and 3.2 m.

below the mean high-tide level. In Fig. 1¹, it is shown that *Macoma* sp. is the most abundant bivalve, attaining a maximum density at a level of approximately 2.2 m. below the mean high-water level. The abundance as well as the vertical distribution of *Mya arenaria* is very limited, and in both these respects there is a marked contrast to the condition existing in the Bay of Fundy area.

Nereis virens, the numbers of which are likewise greatly affected by the soil type, are widely distributed, but we know less concerning their abundance. A soil consisting of sand, mud and decomposing materials is correlated with abundance of this polychaete. At the level of quadrat A1 practically none was observed during the entire survey, whereas at the level of quadrat A3 numbers ranging from four to eight per square metre were obtained. Levels below the mean low-water level gave higher results, namely ten to fourteen per square metre area.

A nemertean, *Cerebratulus marginatus*, was not uncommonly found at a low level, also an unidentified red amphipod (about eight per square metre). Among occasional members of this community occurring at a low level may be mentioned the polychaetes—*Nephtys coeca*, *Haplobranchus atlanticus*², *Amphitrite brunnea*, *Eteone arctica*, *Nainereis* sp., and the nemerteans—*Cerebratulus luridus*, *Lineus ruber* and *Lineus arenicola*³.

The effect of the interaction continually operating between the two biomes briefly described above is commonly evident. For example, a change of certain environmental conditions sometimes favours a heavy set of mussels, *Mytilus edulis*, on clam beds. A rapid increase in the size of the mussel clan favours the development of an entirely new community which so alters the edaphic conditions as a whole that new infaunal forms appear and the clams, *Mya arenaria*, gradually die off. This constitutes true succession applied to marine communities in contrast to direct *development* as defined by Shelford (1929, p. 220).

PART II. PHYSICAL FACTORS OF A SAND BEACH IN THE REGION OF ST ANDREWS, NEW BRUNSWICK.

The intertidal zone of the St Andrews region (Bay of Fundy), because of its unusually wide extent and great diversity of factors controlling community formation, warrants careful study throughout the different seasons of the year.

¹ This figure is based upon class results obtained from a rather intensive study of the beach at Flat Point, near Friday Harbor, Washington. Major credit for the construction of this figure belongs to Miss Mildred Dunlap of the University of Illinois.

² A new species described by Prof. A. L. Treadwell (1932), to whom the writer is indebted for numerous identifications.

³ The second specimen of this species that has ever been recorded. The first specimen was found by Verrill near New Haven about 50 years ago. For this information, as well as for several identifications, the writer is very grateful to Prof. W. R. Coe.

The tidal amplitude (approximately 25 ft. in the St Andrews region and as much as 50 ft. at the head of the Bay of Fundy, which is much greater than almost any other on the north Atlantic coast) is the dominant characteristic of the intertidal belt. Certain environmental factors in this region, such as time of exposure, temperature, salinity, light and evaporation, are greatly modified by the tides in respect to their variations within a very small space.

Shore slope, a factor controlling those mentioned above, in respect to its control of abundance and distribution of many forms, has been determined by recording the time of approach of the flood tide to several arbitrarily selected points. By means of a simple harmonic expression, the curve representing shore slope is obtained. This curve, together with the tide tables, makes possible a calculation of the time of exposure of any particular area with an accuracy sufficient for most biological purposes. The importance of the exposure phase is realised when the dependence of temperature and insolation, or chemical and biological changes, on time of exposure is considered.

The attrition, transport, and gradation of the material on the beach is attributed largely to currents and wave action. These factors are, to a large degree, responsible for the contour of the beach and the grade distribution of its materials and modify such biologically significant features as the depth of the water table, and the porosity of the beach sands.

In this paper there are presented results of a survey of some of the more important physical factors operating upon the seashore, with special reference to the sand beach. Attention has been focused on the data obtained from a definite beach transect through an intensive study of the qualitative character of sand-beach grains, the surface and subsurface temperatures of the beach, the distribution of grade on the beach, the amount of pore space in different grades, the variations in rate of evaporation from the different grades, and the variations in extent of capillary rise through the different grades.

A. QUALITATIVE CHARACTER OF SAND-BEACH GRAINS.

Chemically and lithologically the shore sands of the St Andrews region are not greatly dissimilar in distribution or origin. They consist for the most part of very angular grains of quartz with a coating of iron oxide, felspar, jasper, and a greater or lesser admixture of calcareous matter in the form of fragments of limestone. Obviously, from the unsorted character of the beach sediments and from the similarity of the littoral deposits to those of the undisturbed strata that outcrop along the shore, they have not been washed in by the action of the tides. Their presence may rather be explained as due to the mechanical disintegration of the shore strata by characteristic agencies of marine erosion; and, no doubt, some of the material is reworked glacial debris.

In the region of the sand beaches, the shore strata (according to Bailey, 1917, p. 112) are made up largely of red sandstone and conglomerates of Upper Devonian age. Near transect A, they are noticeable for their brownish red

colour, for their coarseness, and for the fact that they are made up mainly of detritus from the underlying formations, which are of two types, metamorphic rocks and igneous rocks, including granite and rhyolite in abundance. At many points, especially toward their base, these strata are penetrated by intrusive volcanic rocks, dolerite, diabase, and amygdaloid, occurring both as dykes and sills. They are well exposed in this region, the Biological Station having part of its foundation on one of them.

Among the commonest rock types occurring fragmentally as grains and pebbles in the sands of transect A there should be mentioned red sandstone, grey coarse crystalline granites, fine-grained diorite, coarse-grained, slightly porphyritic, basic igneous rocks, vein quartz and quartzite¹.

B. SURFACE AND SUBSURFACE TEMPERATURES OF BEACH.

Inasmuch as the daily and seasonal variations in air temperature in this region are much more pronounced than changes in water temperature (Table II)², their influence on the thermal conditions of the beach during exposure merits more thorough treatment. There are more detailed temperature data available for a nearby beach, differing from the one referred to above chiefly in having a greater proportion of mud. Hence the following discussion is based entirely on this material, collected during 1931.

Table II. *Temperatures taken at the wharf of the Atlantic Biological Station, St Andrews, New Brunswick, during 1931.*

	Mean daily temperature	
	Water (° C.)	Air (° C.)
January	2.96	-6.42
February	1.71	-5.52
March	1.68	0.72
April	3.72	5.34
May	6.63	10.26
June	9.63	14.85
July	12.37	18.22
August	13.23	18.18
September	12.23	13.43
October	10.93	9.52
November	8.58	5.65
December	4.71	-3.37

Data presented in Tables III and IV and Fig. 2 were collected during February, March and November, 1931, at each of the six stations indicated. Temperatures were taken of the air, soil surface and at depths of 2.5, 4, 6, 8, 10 and 15 cm. in the soil. These records were made at various times of the day and night, depending on tidal conditions. The experiments were undertaken

¹ Acknowledgment is due to Drs Christina Lochman and Ray Love for very helpful information about the geology of the St Andrews region.

² Monthly mean water temperatures represent the mean of daily mean temperatures based on the average of two readings taken about 8 a.m. and 5 p.m. Mean air temperatures represent the mean of daily mean temperatures obtained by calculating the mean of the maximum and minimum daily temperatures.

with a view to determining the variation in temperature at several depths at six levels in the intertidal zone during exposure, and the character of the changes in beach temperature following the recession of the tidal waters.

(1) *Temperature variations at different depths and levels of the beach.*

Six stations were selected on the beach—station 1 located on the surface about 3 ft. above mean high-water level, station 2 at about mean high-water level, and stations 3, 4, 5 and 6, each of which is enumerated according to the number of hours ebb tide (Table III)¹. The temperatures presented in this table were taken immediately after the entire beach was exposed, namely from 1.40 to 2.40 p.m., November 5th, 1931, and in the following order: stations 6, 5, 4, 3, 1. During the experiment, the weather was sunny, air temperature 8° C., and temperature of sea water 8.75° C.

Table III. *Temperatures (° C.) at various depths in soil of beach during the time of exposure, November 5th, 1931.*

Soil depth cm.	Stations				
	1	3	4	5	6
Surface	18.50	13.00	13.50	12.50	10.00
2.5	16.25	13.00	13.00	11.75	10.50
4	15.50	12.25	13.00	11.50	10.00
6	14.00	12.00	12.25	11.50	10.00
8	13.50	11.50	11.50	11.25	10.00
10	12.00	10.75	10.50	11.25	9.75
15	11.75	10.00	10.00	10.00	9.50

(a) *Surface temperature of soil in comparison with temperatures of tidal waters.*

It is obvious that tidal waters show very little hourly or daily temperature fluctuation in comparison with the soil surface of the intertidal zone. During the flood tides of summer months, June to August, the beach is suddenly cooled and the incoming waters are slightly warmed by the heated surface layers of the soil. The writer has observed a difference as high as 11° C. between temperature of the soil surface and that of the incoming waters. Furthermore, records have been obtained showing a difference of 2° C. between the surface temperature of the flooding waters nearest shore and that of water 2 ft. deep during flood tide².

(b) *Temperatures at various times of the day.*

The temperatures at any single level on the beach obviously will vary in accordance with the changes in air temperature, time of exposure, moisture content, and other factors. At any period of the day, however, greater constancy is evident in the deeper strata—8–15 cm. Some idea of the sig-

¹ The soil at station 1 consists of fine dry sand and that at station 2 of a coarse grade of sand containing a little moisture below a depth of 2.5 cm. At stations 3, 4, 5 and 6 the soil is composed of mud and sand, the proportion of mud and the moisture content increasing near the low water level.

² More pronounced differences have been recorded by Weymouth (1923) on the Californian coast and Wesenburg-Lund (1912) in the Baltic Sea.

nificant thermal changes throughout the day, during the winter season, in the surface layers and the greater thermal stability at depths below 8 cm. is given in Fig. 2 A. A consideration of the trend of temperature across the beach at several levels clearly shows a pronounced uniformity at stations 3, 4, 5 and 6, in comparison with the higher levels, this uniformity being distinctly more pronounced in the deeper strata (Fig. 2 C). There is apparent a considerable temperature gradient between the surface of the sand and the deep layers. Thus it appears that members of the infauna living near the upper limits of the beach, that is above mean tide level, are subject to a wider range of thermal conditions than those occupying the lower levels at the same depth in the soil.

(2) *The character of the changes in the beach temperatures following exposure.*

To ascertain the changes in temperature occurring in the beach following the recession of tidal waters, records were taken at the same level on the beach at intervals of 10 min., 1 hour, and 3 hours after the tide had receded (Table IV and Fig. 2 B). The experiment was commenced at 2.15 p.m., November 9th, 1931, when the sun was bright and the temperature of the tidal waters 10° C.

Table IV. *Soil temperatures (° C.) following exposure at Station 4.*

Time	Air temp.	Depth in soil (cm.)						
		Surface	2.5	4	6	8	10	15
2.15 p.m.	10.00	8.75	10.00	9.75	9.00	9.00	9.00	8.75
3.15 p.m.	10.00	12.25	12.00	11.50	10.50	10.00	9.75	9.25
5.15 p.m.	9.50	8.00	8.50	8.50	8.75	8.75	8.75	8.75

An analysis of the data indicates that the following temperature conditions obtained: (1) After 10 min. the surface layer was 1.25° C. below that of the sea water (which may be explained as due chiefly to evaporation), the highest temperature was at a depth of 2.5 cm., and below this a gradual decrease took place until at 15 cm. the reading was 8.75° C. No explanation is offered for these latter temperatures. (2) After 1 hour the surface temperature rose to 12.25° C. (bright sun) and that of the lower levels showed a gradual rise from 9.25° C. at 15 cm. to 12° C. at 2.5 cm. This rise is attributed to insolation. (3) By 5.15 p.m. (no sun) the surface layer had cooled down to 8° C. and the deeper strata almost the same amount, the temperature at 15 cm. being 8.75° C. (Fig. 2 B). The dependence of the surface temperatures of the beach on atmospheric conditions is very evident, and the relative stability of temperature in layers below 8 cm. is again shown. The temperature of the beach surface may exceed that of the air. This is due to many factors of which insolation may be considered the most important.

The significance of the subsurface temperature is apparent in the light of chemical and bacteriological processes going on in the subterranean layers and in the existence of numerous underground forms, such as protozoans, annelids, and molluscs.

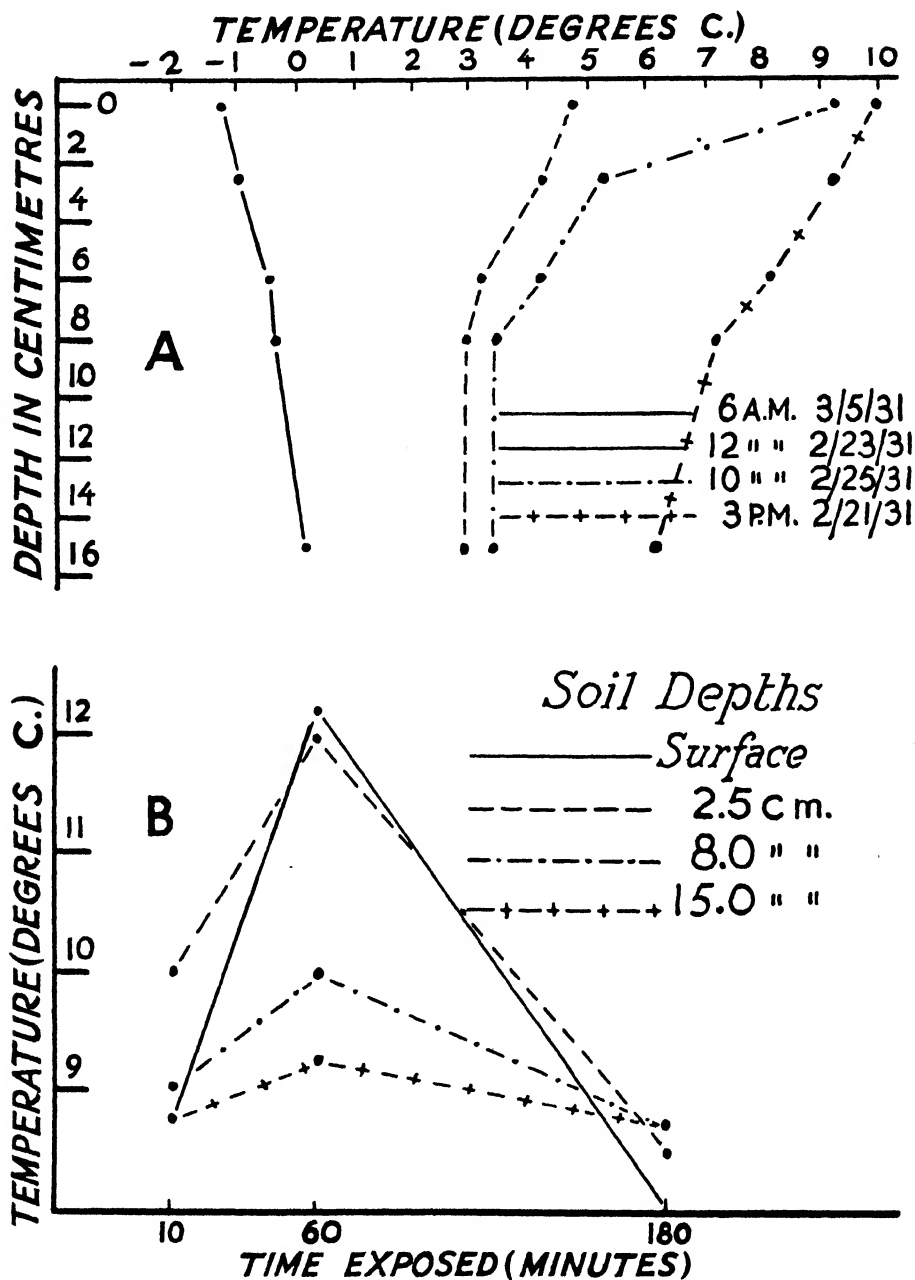


FIG. 2. A. Temperatures during different periods at various depths in soil of beach located near St Andrews, New Brunswick. B. Changes in temperature at various depths in soil of beach following exposure.

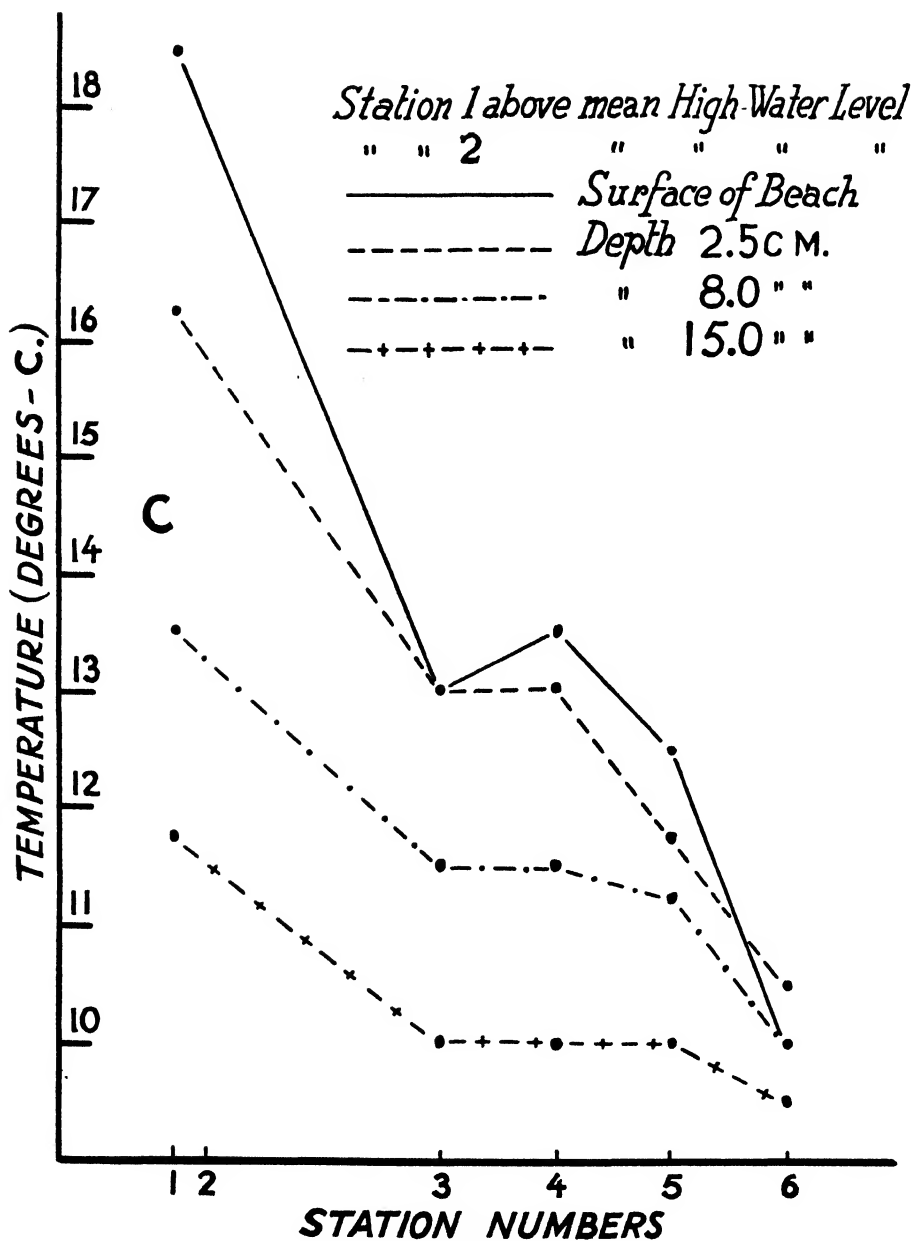


FIG. 2. C. Temperatures at various depths in soil of beach at stations selected in a vertical transect of beach. Stations 3, 4, 5 and 6 are numbered according to the number of hours ebb tide.

C. DISTRIBUTION OF GRADE ON THE BEACH.

Reference has been made to the character of the beach sands in transect A and to their gradation due mainly to tidal influence, to local currents and to the deflection or obstruction of the tidal flow by rock promontories on the shoreline.

In order to determine the relative amount of each grade of sand present, moist samples were collected from three areas of transect A and thoroughly dried in an oven maintained at a temperature of 100° F. They were then separated into their constituent grades by sieving. The sieves employed were of the U.S. Standard Sieve Series and calibrated as is shown in Table VI. Two samples were used from each of the following areas: A1, approximately 18 ft. above chart datum; A2, 13 ft. above chart datum, and A3, 7 ft. above datum. The mean values were calculated, thereby minimising the probable error. The sequence, showing a segregation of the finer grades at the lower extremities of the intertidal zone, is indicated in Table V.

Table V. *Percentage of weight retained by sieves.*

Sand sample	Level above chart datum ft.	Sieve No.					Passing No. 35
		5	7	10	18	35	
A1	18	13.98	4.39	6.92	35.84	38.19	0.67
A2	13	7.38	5.47	6.79	16.99	58.40	4.97
A3	7	2.39	1.48	2.78	15.99	55.17	21.82

Table VI. *Water content, at saturation, of different grades of sand.*

Sieve No.	Normal opening	Normal wire diameter	Water present in 100 vol. of wet sand
35	0.50 mm.	0.29 mm.	44.8
	0.0197 in.	0.0114 in.	
18	1.00 mm.	0.48 mm.	43.2
	0.0394 in.	0.0189 in.	
10	2.00 mm.	0.76 mm.	43.0
	0.0787 in.	0.0299 in.	
7	2.83 mm.	0.92 mm.	43.3
	0.111 in.	0.036 in.	

D. DETERMINATION OF PORE SPACE IN BEACH SAND.

The width of the capillary interspaces is one of the factors which determine the availability of the subsurface water, and, where this is fresh, the salinity of the surface layers of the beach. In one experiment, designed to show the effect of the seepage of subsurface fresh water in the beach, a decrease from 30.9 ‰ to 25.6 ‰ in salt content of the beach water was obtained during exposure resulting from the recession of the tide. Protozoans and other small organisms that inhabit the sand beach are dependent on the liquid film surrounding the sand grains. The determination of the amount of pore space of the various grades of sand on the beach is of considerable ecological significance.

Fifty grams of each grade of dried samples obtained by sieving, as above, were placed in graduated cylinders. Sea water at a temperature of 14° C. was added from a second cylinder that originally contained 100 c.c. After being allowed to stand for several minutes, the supernatant liquid was poured back into the original cylinder, 1 min. being allowed for the draining of the final drops. The volume of the wet sand was recorded, and by calculating the difference from the other cylinder the volume of sea water that it had absorbed was ascertained. The results, which show a slight decrease in the amount of water present due to an increase in coarseness of grade, are expressed in volumes of water per 100 volumes of wet sand (Table VI).

E. RELATIVE RATES OF EVAPORATION FROM DIFFERENT GRADES OF BEACH SAND.

Inasmuch as the temperature of the surface of the sand beach and the availability of the latter as a habitat for the organisms which live in the water film around the sand grains are affected by the rate of evaporation from the surface layers, an effort was made to determine the rate of evaporation from an ungraded sample, and also from samples of the different grades by the following methods, which are essentially similar to those employed by Bruce (1928) at Port Erin, Isle of Man.

Dishes containing the graded samples of sand saturated with sea water, but in fully drained condition, were exposed in a room of practically constant temperature and humidity. The Petri dishes used were 9.6 cm. in inside diameter and the sand layer was about 9 mm. thick, so that each exposed to evaporation a surface area of 112.4 sq. cm., the surface exposed being obviously of greater importance than the absolute weight of sand used. The loss of weight was ascertained periodically and is expressed in grams per 100 sq. cm. of surface at successive stages of drying (Table VII).

The results indicate a significant variation in the rate of evaporation between the grades employed, a maximum difference of 18.6 per cent. occurring after 3½ hours and of 8.1 per cent. after 13 hours of exposure.

Table VII. *Effect of grade upon rate of evaporation from the surface of wet sand.*

Sieve No.	Loss of water in grams per 100 sq. cm.				
	3½ hours	5½ hours	8½ hours	10½ hours	13 hours
-35	7.0	10.2	14.6	17.1	20.1
35	6.9	9.8	14.0	16.6	19.6
18	6.6	9.5	13.6	16.3	19.3
10	5.9	8.9	13.0	15.6	18.6
Ungraded	7.3	10.9	15.1	17.7	20.6

Temperature of sea water used 21.5° C. Range of humidity 17–28 %. Room temperature about 27° C.

F. RATE OF CAPILLARY RISE OF WATER THROUGH BEACH SANDS.

Corresponding to the water table of cultivated lands there are in the intertidal zone, subsurface reserves, the quantitative rhythmic variation of which is influenced by evaporation. These subsurface reserves may consist of sea water infiltrated from the margin of the tide, or of fresh water from the land wash. Clearly, the amount of these that reaches the surface depends first on their quantity and depth, and, secondly, on the degree of capillary rise through the sandy layers above. The subsurface reserves in the area studied are at a depth of about 0.3 m., and it was considered significant to determine the rate at which the water is able to rise through the capillary channels.

Table VIII. *Effect of grade of sand upon height of capillary rise, expressed in millimetres.*

Time interval	Mesh - 35	Mesh 35	Mesh 18	Mesh 10
8 min.	36	23	16	14
20 "	46	27	18	15
1 hour	56	30	24	18
3 hours	66	36	32	22
5 "	71	41	35	25
7½ "	74	45	38	28
15½ "	79	48	39	31
19½ "	81	50	42	33
26½ "	84	54	44	41
42½ "	89	58	49	42
51 "	92	60	51	43
66½ "	95	65	55	50
76½ "	100	67	56	51
95½ "	104	70	63	55
120½ "	111	76	65	60
147 "	112	79	70	68
174 "	115	82	75	70
198 "	120	90	80	71
221½ "	122	92	81	72
235 "	123	92	81	72
271 "	127	99	85	81
296 "	130	101	89	84
321 "	133	105	94	86
332 "	136	106	95	90
364 "	138	107	98	91
432½ "	141	113	100	92
510½ "	151	118	107	100

The rate of rise through sand samples of different grades and also through ungraded samples was determined in the following way. A series of glass tubes open at both ends, 11 mm. in inside diameter, was fixed in an upright position by means of a wooden frame, their lower ends resting in a large Petri dish with a flat bottom. The tubes were nearly filled, each with a certain grade of sand, and a sample of sea water was poured into the dish to a depth of 7 mm., which depth was maintained throughout the course of the experiment. The temperature throughout ranged between 15 and 17.2° C., while the room temperature ranged from 19 to 21° C. Errors due to differences of packing are such as to render it probably impossible to get results to check within the range of insignificance. Nevertheless, it is seen that the height to which the water column rises per unit of time is a direct function of grade and tends to

increase as the sand grains decrease in size. It will, obviously, be affected by any solutes that may be present in the water. It was found that the values obtained in the case of the ungraded sample were about midway between those of the -35 and 35 grades. In Table VIII it is shown that at the end of the experiment, that is, after about 510 hours, the heights obtained in the four grades (meshes of -35, 35, 18 and 10) were 151, 118, 107 and 100 mm. respectively. Bruce (1928, p. 549) employed much finer grades and consequently obtained higher results per unit of time. This author states that it is not apparent that the differences of surface tension between fresh water and sea water, or between two samples of the latter from different sources, result in any constant or significant differences of capillary rise.

SUMMARY AND CONCLUSIONS.

PART I.

Two major biotic communities of the Bay of Fundy region are described and the predominant components discussed in light of their ecological relations.

1. The major infaunal community of the intertidal zone is the *Balanus-Littorina-Fucus* biome, occurring not only throughout the Bay of Fundy, but in the entire Gulf of Maine and probably ranging north to Newfoundland.

2. The *Balanus-Mytilus edulis* association of the beforementioned biome prevails in the region of St Andrews, New Brunswick, where the vertical range of this major community is from the mean low-water level to the mean high-water level, approximately 28 ft. above chart datum. The downward range is restricted by predatorial action of dominants of a subtidal community, the *Strongylocentrotus-Asterias* biome.

3. The occurrence of true succession in the case of the growth of the *Balanus-Mytilus edulis* association has been described.

4. The extent of seasonal changes in abundance and distribution of certain predominants of the *Balanus-Littorina-Fucus* biome is shown in Table I.

5. A new polychaete, described by Prof. Treadwell under the name of *Haplobranchus atlanticus*, is reported. Specimens were found growing in considerable abundance at the place of attachment of *Fucus vesiculosus*.

6. A nemertean, *Lineus arenicola*, the second specimen of this species that has been recorded, is listed for the St Andrews region.

PART II.

Transect A of a sandy beach located near the Atlantic Biological Station, St Andrews, New Brunswick, has been investigated with particular reference to several physical factors of distinct ecological importance.

1. The predominant factor is the extremely high tide which modifies the incidence of practically all the other factors. The segregation of fine grades of sand at the lower extremities of the intertidal zone, as indicated by Table V, is attributed to currents and wave impact, largely controlled by tidal forces.

2. The shore strata are composed chiefly of red sandstones and con-

glomerates of Upper Devonian age. The most common rock types occurring fragmentally as grains and pebbles in the sands of transect A are red sandstone, grey coarse crystalline granites, fine-grained diorite, coarse-grained slightly porphyritic basic igneous rocks, vein quartz and quartzite. The sand grains originate from the mechanical disintegration of the shore strata by characteristic agencies of marine erosion.

3. During the summer season the sand beach undergoes pronounced sudden changes of temperature, a difference of 11°C . having been observed between the soil surface temperature and that of the incoming waters.

4. A marked temperature gradient exists, especially during the summer season and at the upper levels, between the surface of the sand and the deeper layers. During exposure, the beach temperatures at depths between 8 and 15 cm. are relatively stable.

5. The water content, at saturation, of the different grades of sand employed exhibits little variation, the average amount being approximately 44 volumes in 100 volumes of wet sand.

6. The effect of size of sand grains on the rate of evaporation is appreciable, the maximum difference obtained after an exposure of 13 hours being about 8 per cent.

7. Variations in the grades of sand observed have been found to exert marked influences upon the rate of evaporation from exposed areas of the intertidal sand beach.

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ZONATION OF VEGETATION ALONG RIVER COURSES

By J. G. MYERS, Sc.D., F.R.E.S., F.Z.S.

IN the ecological literature available to me in Trinidad I have sought in vain a term for, or even a description of, a phenomenon which is very marked in rivers of Guiana and Venezuela. I allude to a distinct zonation in the bank vegetation along the course of a river from its upper reaches to its mouth¹. I suppose the neglect of this interesting ecological feature is due largely to the fact that, in most parts of the world, streams which still retain primitive vegetation along their entire course are extremely rare. In the north-eastern part of South America they are, however, frequent, especially among the smaller rivers and creeks. Richard Schomburgk's observations here nearly a century ago show that he recognised this succession of plant communities. Unfortunately an adequate description is rendered almost impossible by the prevailing ignorance of the floristic composition of rain forest in this area—an ignorance which is now being dispelled by the efforts of the Forestry Officers of British Guiana and of Trinidad.

By zonation along the course of a stream I mean a definite succession of plant communities in space, determined not by edaphic factors encountered in the area through which the river flows, but by factors dependent on the stream itself, such, for instance, as its width in a given place or the distance from the sea; and thus recurring in an essentially similar sequence in all the streams of the region, where modification by man has not obscured it. Thus the spatial succession of forest and wet savannah along the courses of many of these streams, being due to local soil or physiographic factors or to conditions not necessarily produced by the river itself, is not included in this discussion.

The following, unfortunately very sketchy, observations have been made in the Delta of the Orinoco, in the North-West District of British Guiana, and on the Coppename River in Dutch Guiana.

In 1929 (*Kew Bull.* 1930, pp. 1–10) in an account of a visit to a stand of wild cacao, I briefly noted the changes in the vegetation along the course of the Coppename River. This is a good example, since, although a large river, it has never, I believe, supported the smallest white settlement, while its small and entirely negligible Indian and bush-negro population is grouped in three tiny hamlets and one or two scattered camps. The river is, in fact, almost uninhabited, and its vegetation primitive along the whole course. Briefly summarised, the bank vegetation along the lower course consists predominantly

¹ Zonation from the water to the upper parts of the banks has been well described in widely separated regions, but longitudinal zonation is not, for instance, mentioned in Butcher's extensive paper on river ecology (1933), nor in his bibliography of forty-one titles.

of mangroves (*Rhizophora mangle*), with occasional patches of *Drepanocarpus lunatus*. A few miles from the mouth, tall *Montrichardia* appears among the mangroves. About the mouth of the Tibiti Creek (say some 40 miles from the sea) the mangrove loses its dominance and is replaced by *Drepanocarpus*, backed by luxuriant *Montrichardia*. Soon after, the water front begins to be occupied by low trees of *Pachira aquatica*, interspersed with stretches of *Montrichardia*, sometimes bordered by beds of *Crinum*. Later a species of *Inga* appears as a fringing bush, and the stretches of *Pachira* are varied with trees of *Pterocarpus draco*. This type of bank vegetation eventually gives place to a much more mixed assortment of rainforest trees (from which *Pachira* has disappeared), heavily draped with dense curtains of creepers, but in places shrubs and small trees of *Inga* sp., in almost pure consociation, form a very different border.

The lower Waini River, in the North-West District of British Guiana, is settled by occasional grant-holders, who have, however, done little to modify the actual riparian vegetation, which, from the mouth upwards, for many miles, consists of an unbroken fringe of mangroves (*Rhizophora mangle*), many of them large trees. Loranthaceae are abundant, an occasional creeper and a large Bromeliad (*Aechmea* sp.). About 15 miles from the sea, occasional manicole palms (*Euterpe edulis*) appear. The dominance of mangroves continues till a tributary stream, the Baramanni, is reached, though there are here and there patches of *Drepanocarpus lunatus* on the water front, and *Pachira aquatica* and *Pterocarpus draco* begin, later becoming dominant on the Baramanni about 90 miles from the sea. In the forest behind them *Euterpe edulis* is dominant, while in front they are draped in places with *Allamanda cathartica* and a pink-flowered *Bignonia*. *Montrichardia arborescens* and *Pentaclethra filamentosa* appear, and the last mangrove is left behind soon after entering the Biara creek. From this we eventually branch off into the Barabara, a very narrow creek, where some *Pterocarpus* still occurs, but the *Pachira* has disappeared, the riparian forest becomes much more varied, the fringe of creepers is absent and one sees a long way in between the trees, where the water extends some distance from the inundated banks. Thereafter is a succession of wet savannahs and of forest patches, till the Moruka River is reached by a connecting passage.

The Barima river runs somewhat parallel to, but farther inland than, the Waini. I do not know its lower course, but at the point where it is joined by the Mora Passage, from the Waini, at about 50 miles from the sea, mangroves (*Rhizophora mangle*) dominate the bank vegetation. They continue dominant for about 35 miles, with plentiful trees of *Pterocarpus draco*, and then begin to thin out, finally disappearing some 10 or 12 miles farther, about the mouth of the Morebo Creek. The *Pachira aquatica*, which has been scattered with increasing frequency among the mangroves, becomes dominant, with, in places, *Montrichardia arborescens* and still many *Pterocarpus*. As in most of

this lower region, the forest behind the fringe is *Manicaria-Euterpe* swamp forest. Later, about the mouth of the Anabisi creek, tall forest trees, chiefly *Mora* (*Mora excelsa*) overtop the *Euterpe* palms, while the trees of the fringe become much more varied, *Pachira* less abundant, and the whole is hidden beneath a dense curtain of multifarious vines and creepers, flowering and leafing luxuriantly. *Pachira* disappears completely, and *Montrichardia* becomes scarce, as the earth banks show above the water, in contrast to the inundated margins of the lower reaches. *Costus* spp., *Heliconia*, *Piper* spp., *Pentaclethra filamentosa*, *Ischnosiphon*, *Inga*, join the bank medley, under the shade of the tall moras. Schomburgk (1922, trans. vol. 1, 87, 102, 136, 141, 147-8) well describes this succession on the Barima River.

On the Amakura River, which flows through the delta of the Orinoco, the mangrove zone is succeeded upriver by a dominant *Pachira-Pterocarpus* association, often hidden by dense bank curtains. *Rhizophora* disappears much sooner on the right bank than on the left, and is sometimes associated with *Drepanocarpus lunatus* beds. A more interesting association is afforded, however, by the large floating grass beds. These, intermingled with *Eichhornia* spp., break loose to form huge floating islands which sweep up and down with the tide, but in their original form are fringing beds. While the water-hyacinths occur almost continuously through the mangrove and *Pachira-Pterocarpus* zones, the grass beds are sharply restricted, those of *Panicum elephantipes* to the former, and those of *Paspalum repens* to the latter, an intervening stretch forming a kind of no-man's-land (ecotone) where neither grass occurs. On the lower Yarikita, which flows into the Amakura in the *Pachira* zone, *Paspalum repens* beds are frequent and luxuriant. On the Carapo creek, which enters lower down, in the transition zone, beds of *Panicum elephantipes* and of another water-grass, *Hymenachne amplexicaulis*, appear as soon as one enters the mouth, followed by rare patches of *Paspalum repens*, but the *Panicum* continues further up, in small and scattered beds. On the Awaracaba creek, flowing into the Amakura still further downstream, both the *Panicum* and the *Paspalum* are practically absent. In both these creeks, the *Pachira-Pterocarpus* zone takes possession as soon as one enters the mouth, the Awaracaba showing considerable intermixture with *Pentaclethra*, *Euterpe*, *Moronobea coccinea*, *Manicaria*. In both creeks this zone speedily gives place to swamp forest¹, with no distinctly differentiated bank fringe, and occasional wet savannahs dominated by a tall, stout *Rhynchospora* sedge.

The distance to which the mangrove zone extends upstream is doubtless determined by the influence of brackish water, and this, in its turn, in these uniformly sluggish streams (slow, that is, in their lower reaches), depends chiefly on the size of the river. There is some slight evidence of an extension of the mangrove zone by the deepening of the Mora Passage which connects

¹ This is either *Manicaria saccifera* (truli) swamp, or one with few or no palms and a predominance of stilt-rooted small trees, especially *Moronobea coccinea*.

the Barima with the Waini near the mouth of the latter. This is now a wide channel, scoured by tidal water through both rivers, and regularly passed by fairly large coastal steamers. It is lined by mangroves (*Rhizophora*) almost exclusively, but some *Pterocarpus* comes in towards the upper end and a little weedy *Montrichardia*. In 1841, when the Mora Creek was a narrow passage not navigable by sailing-vessels, Schomburgk (1922, trans. vol. 1, 87) observed that: "The more we widened our distance from the coast, the rarer became the specific coastal vegetation. The *Avicennia*, *Rhizophora* and the *Conocarpus*¹ had long disappeared when, just about five miles above the exit of the Mora into the Barima, we reached the mouth of the muddy and yellow Aruka. . . ." At the present time *Rhizophora*, as a dominant, extends farther up the Barima for about 35 miles, up the Aruka itself to the mouth of the Koriabo and up this tributary some 9 miles more. Schomburgk's testimony, quoted above, is decidedly definite, but is unfortunately contradicted equally definitely by his own statements later on, of mangroves extending up the Barima practically as far as I saw them, namely about the mouth of the Morebo Itabo (1922, vol. 1, 137, 141). Another feature associated, perhaps causally, with the distribution of the zones is the colour of the water and the differing characters which that indicates. These streams, where they flow through high forest, and some distance into the *Pachira* zone, are typical black-water² creeks, but lower down, in the mangrove zone, they become muddy and yellow with earthy sediment, owing probably to tidal action.

SUMMARY.

All these streams flow through a more or less definite, somewhat overlapping sequence of plant communities, as represented by the bank vegetation, which may be summarised as follows, from the upper reaches to the mouth.

(1) Tall rain forest with no differentiated bank fringe. This occurs chiefly on the larger rivers, at a considerable distance from the sea.

(2) Swamp forest, with no differentiated bank fringe.

(3) A zone of mixed bank vegetation, smothered by a dense curtain of creepers.

(4) *Pachira-Pterocarpus* zone, on the Amakura and Yarikita associated with *Paspalum repens* grass beds.

(5) *Rhizophora* zone, associated on the Amakura river with *Panicum elephantipes* grass beds.

Until quantitative ecological research, with the measurement of physical factors, gives us more definite information, the factors influencing zonation may be tentatively suggested as follows:

(a) *Width of the stream.* Where this is small, the actual watercourse forms a narrow defile, shaded by the forest walls, and insufficient light penetrates to

¹ The *Avicennia* and *Conocarpus* about the Waini mouth occur behind the *Rhizophora* fringe.

² Very clear water stained with vegetable matter to a yellow colour, which in bulk appears black.

permit the formation of a leafy creeper curtain. Taller forest may, of course, produce the same result on a wider river.

(b) *Character of the water*, whether black or muddy. This is at least partly dependent on (c). It is well known that in the Amazon system, quite independently of tidal influence, the vegetation of the yellow water (e.g. main Amazon), clear or blue water (e.g. Tapajoz) and black water rivers (e.g. Rio Negro) is strikingly different. I hope later to show the effect of the difference of water on the flora of aquatic and riparian grasses.

(c) *Distance from the sea*. The extent of salinity is a function of this and of the size of the river, and is probably the deciding factor in the mangrove zone.

Differences in elevation above sea-level can hardly be significant in this generally lowlying region.

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CONTRIBUTIONS TOWARDS A SURVEY OF THE PLANTS AND ANIMALS OF SOUTH HAVEN PENINSULA, STUDLAND HEATH, DORSET

II¹. GENERAL ECOLOGY OF THE FLOWERING PLANTS AND FERNS

By RONALD GOOD.

(With Plates XXIII–XXVII, a folding Map, and three Maps
and two Diagrams in the Text.)

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¹ The first number of this series, by C. Diver, was published in *Geogr. J.* **81**, 1933.

INTRODUCTION.

POOLE HARBOUR, the great lake-like estuary that receives, through the rivers Frome and Piddle, the drainage waters of all central Dorset, is almost cut off from the sea by two opposing necks of land. These run north and south, leaving between their extremities a narrow opening (about one-quarter of a mile wide) and they are now connected by the operation of a steam ferry. The northern, and very narrow, neck is known as Sandbanks, and is now almost completely built over. The southern, and broader, neck has so far almost escaped human interference, and it is this area which is the subject of this series of ecological studies. It has no generally accepted and accurate name, and for present purposes it has been designated South Haven Peninsula, a name taken from its northern extremity, South Haven Point, and conveying a concise notion of its geographical nature.

South Haven Peninsula has long been known to botanists (under the less exact names "Little Sea" and "Studland Heath") as a classic collecting ground, as well for the richness of its flora as for the rarities it contains. Interesting as these may be, it is, however, quite another, though related, consideration which makes the area specially worthy of careful study. This is the circumstance that through a combination of events which, to say the least, must be most unusual, the Peninsula to-day affords a remarkable opportunity for the investigation and elucidation of certain aspects of plant establishment and plant succession and for the comparison of similar habitats at different stages of vegetational development.

The object of this paper is to describe and, as far as possible, to analyse the vegetation of South Haven Peninsula as it existed in 1932-3. It will, it is hoped, fulfil the three useful purposes of forming a descriptive datum from which subsequent changes can be assessed; of giving an indication of the factors which are operating or have operated to control the vegetational development; and of arousing interest in some of the innumerable problems which still await investigation.

So far South Haven Peninsula has been little modified by man, but this undisturbed condition is unlikely to continue for long. Some eight years ago a motor road was constructed over the peninsula converting it from a remote and rather inaccessible region into what is rapidly becoming one of the main outlets for the great urban populations of Poole and Bournemouth. Up to the present the effect on the wild life has been small, but even if the most obvious danger of building is long delayed it is almost certain that the future will see a gradual lessening in the opportunities for that adequate ecological survey which the peculiar interest of the area merits, and which it is the object of this series of publications to provide.

The nomenclature used in the present paper is, with two exceptions, that of the Eleventh Edition of *The London Catalogue of British Plants*, 1925. The

exceptions are the use of the names *Psamma arenaria* and *Statice Limonium* instead of *Ammophila arenaria* and *Limonium vulgare*, the reason being that the former have already been employed by Diver in publications dealing with South Haven Peninsula. The name *Betula alba* is used in its widest sense to include *B. verrucosa* and *B. pubescens*. Both these are present on the peninsula, but their respective distributions have not yet been studied.

THE HABITAT.

GEOGRAPHY.

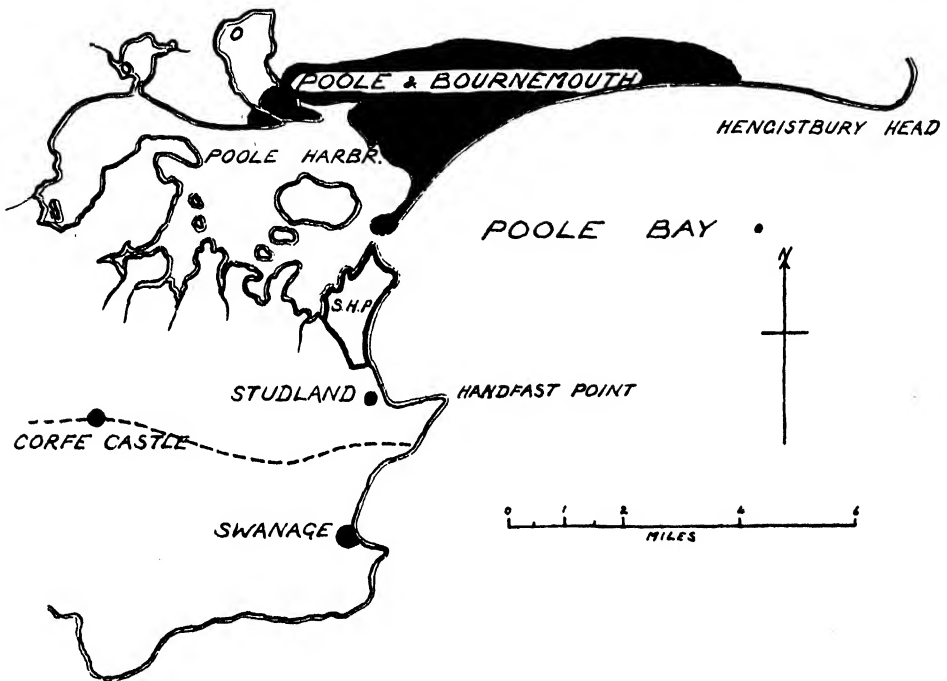
South Haven Peninsula is a narrow, fairly level, low promontory running north-north-east from a point about half a mile north of the village of Studland and forming the southern arm of the narrow entrance to Poole Harbour in the county of Dorset. Its eastern or seaward edge forms the northern portion of Studland Bay, and its western edge is part of the south-eastern shores of the harbour. At the north it tapers rapidly into a sandy projection called South Haven Point, and in the south its base passes imperceptibly into the great heath north of the Purbeck Hills. For scientific purposes it has been necessary to delimit the peninsula on the south somewhat artificially, and this has been done by taking as the boundary in that direction, first the old track running south-east from Brand's Ford to the new road, thence the new road from the track junction to a point just north of Knoll House and thence the rough road running east from the latter point to the sea. The peninsula so delimited is almost exactly two miles in maximum length, just under one mile in maximum breadth, and has an area of about $1\frac{1}{4}$ square miles. The whole lies between the longitudes $1^{\circ} 56'$ and $1^{\circ} 59'$ W. and within the latitudes $50^{\circ} 39'$ and $50^{\circ} 41'$ N. It falls within the co-ordinates 1002-1005 E.: 1200-1205 N. of the new National Grid and is covered by the following Ordnance Survey Maps: 6-in. Dorset, sheets LI N.W. and LI S.W. ed. 1925 (all but the extreme north tip is on the latter): 1-in. Coloured Edition, sheet 144: 1-in. Popular Edition, sheet 141: 1-in. Geological Survey, sheets 329 and 343: and Geographical Types, Series 1, Land Forms.

It has been necessary to give names to many of the minor topographical features of the peninsula. This has been done by Diver and myself in collaboration and a special map embodying these, and also the lines of the National Grid, has already been published by the former.¹ By the courtesy of the Royal Geographical Society this map is reproduced here.

¹ **Diver, C.** "The physiography of South Haven Peninsula, Studland Heath, Dorset. Being No. 1 of a series of 'Contributions towards a survey of the plants and animals of South Haven Peninsula'." *Geogr. J.* **81**, No. 5, 1933.

TOPOGRAPHY.

South Haven Peninsula is easily described topographically, since it consists of three obvious and distinct parts. The western part (the Western Plateau) is a long narrow level area of deposits belonging to the Bagshot series of the Eocene formation. The eastern part (the Eastern Sands) is composed of a series of sand ridges running roughly north and south and of comparatively recent deposition (see *infra*) through the agencies of wind and water. Between these two parts, in the southern part of the peninsula, is a considerable body of open water known as Little Sea.



MAP 1. Sketch-map of the Poole Harbour district showing the position of South Haven Peninsula (heavy outline).

The Western Plateau dips gradually from south to north, and at its former extremity includes the summit level of the whole peninsula in a small zone just exceeding the 50-ft. contour. Its surface contains no very marked features, but its western or harbour edge is much indented, giving rise to a series of bays.

The Eastern Sands consist essentially of three parallel ridges of sand-dunes, together with the various depressions and slacks between them. In the south these slacks are less marked and the ridges tend to coalesce. In the north the two main depressions between the three ridges are known respectively as Central Marsh (the western) and Saltings Strip. South of the latter is a large expanse of shallow water called Eastern Lake.

Throughout most of the centre and south of the peninsula the Western Plateau and the Eastern Sands are separated by Little Sea, and the original eastern edge of the plateau is now the western shore of the lake, but on the north and extreme south the separation is by no means clear, because the ends of the plateau are to some extent overlaid by a varying amount of blown sand from the east. As far as can be determined, however, the old eastern edge of the plateau north of Little Sea roughly follows a line along or just east of the new road and extended as far north as Gravel Point. In the south the old plateau edge approximately follows a line drawn from the extreme southern point of Little Sea to, and including, a pronounced local elevation just west of Pipley Pool 3.

The elongated and irregularly shaped lake, Little Sea, is shallow and has a comparatively level bottom, mostly of clean sand but with local patches of mud. Its bed actually represents the original valley or slack formed between the first-deposited sand ridge and the Western Plateau. The average depth of Little Sea is from 2 to 3 ft., and in many places it can be waded, but here and there are between 4 and 6 ft. of water. It receives three main sources of land drainage: one, the smallest, at its extreme north end; a second, near its centre, from the Western Plateau; and a third, by far the most important, from the main valley of Studland Heath away to the south-west.

At South Haven Point and along Shell Bay is a small collection of temporary wooden buildings, occupied, with one or two exceptions, during the summer months only. Along the shore edge also, in the extreme south-east of the peninsula, there is a row of small huts. Various small brick or stone buildings have from time to time existed on the area, but the last of these was abandoned in 1914 or thereabouts, and most of them have entirely disappeared. The remaining evidences of human activity are: the structures connected with the steam ferry at South Haven Point; the new road, which skirts Little Sea closely on the west; the remains of former agricultural enclosures (of small total area); certain dykes and drainage cuts; and the artificial Redhorn Quay.

GEOLOGY.

The nature of the Bagshot beds composing the Western Plateau is best seen from the series of exposures in the shallow cliffs along the edge of the harbour shore. From these it appears that the slightly more elevated southern part of the plateau is largely built up of a coarse yellow ferruginous sandstone of a fairly soft nature, while the northern and rather lower part is mostly reddish clay, but the division is not absolute and patches of clay are widely scattered. The sandstone is conspicuous about Redhorn Bay where the cliffs reach 10 ft.: the clay is well seen at the head of Bramble Bush Bay and in Plateau Bay. A thin layer of gravel extends over much of the surface of the plateau, and is generally overlaid by a very thin peat layer.

At one point on the harbour shore there is a small and quite localised

sand-dune (Sandy Point), still partly mobile. The genesis of this dune is a mystery, but it clearly has no organic relation with the rest of the Western Plateau and is presumably of the same nature as the Eastern Sands.

The harbour shore itself varies from almost pure gravel to pure mud according to the relative amounts of gravel, cliff debris and harbour silt present.

With the exception of the extreme northern part of Central Marsh which is formed of harbour silt, the whole of the Eastern Sands as well as most of the bed of Little Sea is built of a very homogeneous marine sand of recent deposition (see history below), and, as has been said, this also overlies the Tertiary deposits of the Western Plateau in two areas. This sand is extremely clean, fairly fine in texture, and almost white in colour. In places, as in Shell Bay, it contains a good deal of molluscan shell debris and locally it gives the phenomena known as "singing sands".

In the course of the work here described numerous soil samples were taken. The analyses of these samples will be more conveniently considered elsewhere, and only the more outstanding features are mentioned here.

In general there are present two kinds of soil. On the Western Plateau there is developed a podsol, the upper layers of which consist of almost completely bleached sand. This is made up very largely of silica, with small amounts of iron and aluminium compounds. The reaction is acid, as is usual in such soils, and there is, normally, never more than a trace of calcium. Below the upper leached layer the soil passes into the unaltered Bagshot sands and clays.

Throughout the Eastern Sands the soil, for an indefinite depth, consists of a homogeneous deposit of clean silver-grey sand. This, like the soil of the plateau, consists almost entirely of silica and, also similarly, contains but a very small amount of calcium. As first deposited it contains practically no combustible material, but this increases steadily as plant colonisation proceeds.

Both in general appearance and in plant covering these two soils show a marked similarity, and examination shows that they are, indeed, very much alike, each being characterised by a very high proportion of pure silica, by a marked poorness in mineral salts, by an appreciable amount of iron and by an almost complete absence of calcium, resulting in an acid reaction.

This similarity is one of the most interesting features of the peninsula. The great bay which extends from Handfast Point to Hengistbury Head has been chiefly carved from the widespread local Bagshot beds, and both the rivers draining into Poole Harbour pass through such deposits for parts of their courses. In view of this there can be little doubt that the sand deposited in the Eastern Sands of the peninsula is derived from the denudation of the Bagshot beds elsewhere, and hence that there is between the materials of the Western Plateau and those of the Eastern Sands not only a close similarity but also an actual community of kind and origin.

CLIMATE.

There is no meteorological station on the peninsula, but those at Bournemouth, Poole and Swanage are all about 4 miles distant in different directions. For much of the following information I am indebted to the Town Clerk of Bournemouth, the Borough Engineer of Poole and Mr Wright of Swanage.

Rainfall.

According to the Rainfall Atlas of the Royal Meteorological Society the average annual rainfall on the peninsula over the years 1868–1923 was approximately 30 in., with extremes of 42 in. in 1872 and 17·5 in. in 1921.

Other average annual figures are:

Bournemouth (1893–1932), 32·2 in. Extremes 42·2 in. in 1915: 17·5 in. in 1917.

Poole (1929–33), 27·9 in. Extremes 29·9 and 22·5 in.

Swanage (1928–33), 27·9 in. Extremes 34·1 in. in 1928: 20·6 in. in 1933.

Temperature (° F.).

According to Bartholomew's *Physical Atlas* the figures for the peninsula during the latter part of the nineteenth century were:

Annual average, 51°: average annual range, 21·5°.

Monthly averages: highest in August, 62·5°: lowest in January, 41°.

Other figures are:

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean	Extreme	
														Max.	Min.
Bournemouth (1893–1932)	41·2	41·4	45	47·8	53·1	58	61·7	61·5	58	52	45·7	43	50·8	—	—
Swanage (1931–3)	42·5	40	42·5	46	52	58	60	62	58·5	54	47	41·5	50·3	85	21

Sunshine.

The peninsula falls within the area of highest sunshine values in Great Britain, only parts of Devon, Cornwall and the Isle of Wight having higher average figures. Annual average figures are:

Bournemouth (1893–1932), 1840 hours. Extremes 2137 hours in 1911: 1375 hours in 1898.

Swanage (1928–33), 1822 hours. Extremes 2058 hours in 1933: 1597 hours in 1932.

Wind.

The prevailing wind is from the south-west and for Swanage (1929–33) this is recorded on about 30 per cent. of all days. Most of the rain comes with this wind. North-east wind occurs on about 20 per cent. of days and the least common is north, on about 5 per cent. of days.

HISTORY.

The sequence of events by which South Haven Peninsula has reached its present dimensions and outline has already been described exhaustively by Diver (*loc. cit.*), but it is desirable to give here a very brief summary of that account in order that the relations between the three main topographical features of the area may be understood.

In the seventeenth century, and for an unknown length of time previously, the peninsula consisted solely of the long narrow neck of land of Bagshot beds now known as the Western Plateau and the seaward shore closely followed its eastern edge. Towards the end of that century, or early in the next, a great change began, marked by the accumulation of marine sand against this eastern edge. This gradual deposition of sand has continued till to-day and is still proceeding and has resulted in the formation of the wide area known as the Eastern Sands. The deposition has taken the form of a successive formation of a series of sand ridges roughly parallel to the original peninsula, and these have had the important effect of interfering with and finally completely blocking the escape of much surface drainage water from the Western Plateau, so that this has become dammed up to form what is now Little Sea. This is the essential outline of the story. For further details Diver's paper should be consulted, although many of them are incorporated in the account on a later page introductory to the vegetation of the Eastern Sands.

THE VEGETATION.

GENERAL DESCRIPTION.

From the vegetational point of view, as well as from the topographical, South Haven Peninsula is divisible into three distinct regions, but these do not correspond. The differences are first, that the harbour shore, while scarcely a separate topographical unit, supports a very distinct vegetation, and, second, that the vegetation of Little Sea cannot be reasonably separated from that of the remainder of the new habitats which have resulted from the gradual accumulation of the Eastern Sands. The basic vegetational divisions are therefore the harbour shore, the Western Plateau and the Eastern Sands, including Little Sea.

The first of these is very distinct, consisting for the most part of species found in neither of the other divisions. These latter, on the other hand, are fundamentally similar in kind, but differ much in detail and developmental condition. The relation between these two is, in fact, one of the most interesting features in the botany of the peninsula and may be expressed simply by saying that in the one there is shown the ultimate vegetational equilibrium towards which the various successive trends of the other are converging. That is to say there are to be seen side by side not only the final condition but also many of the stages in the gradual process by which this has been reached.

Actually each of the three divisions has a different developmental status. The vegetation of the harbour shore and that of the Western Plateau may be described as climax vegetations in the sense that they are practically stable, but there is an important difference between them. The former is, for the most part, salt marsh, a type of vegetation in which edaphic factors, especially the salt content of the substrate, play a predominant determining role. The vegetation of the Western Plateau is heath (of a slightly damp kind), a type of vegetation in the determination of which climatic conditions are of much greater relative importance, and similar heath is the natural plant-cover over much of the Tertiary deposits of the Hampshire basin. That such deposits bear this particular kind of vegetation is, however, chiefly the result of the prevailing climatic conditions. Thus, while the harbour shore vegetation must be regarded as an edaphic climax type, that of the plateau may more properly be called a climatic climax type. Another consideration serves to emphasise this difference. Both are practically static, but the changes necessary to lead to an alteration in the nature and distribution of the vegetation along the harbour shore are clearly much less drastic than those required in the case of the plateau. Minor variations in tidal values or in the relative levels in land and water or even the marked accumulation of debris from the adjacent land would be sufficient to disturb the equilibrium in the shore, while the vegetation of the plateau is not likely to suffer much disturbance unless there is considerable change in climate or a cataclysmic orographical change.

The state of the vegetation over the Eastern Sands, on the other hand, is quite different, in that it is, with few exceptions, everywhere dynamic. These exceptions are in certain of the oldest parts (first deposited) of this region where the vegetation has attained a condition closely resembling that of much of the Western Plateau. Nevertheless it may well be that even in these places the plant covering has not in all respects reached a state of equilibrium.

The vegetation of these sands is so varied and complex that a full description of it must be deferred till later (see p. 379). It may, however, be outlined here by saying that it consists essentially of the various stages of a xerosere commencing with the deposition of sand of marine origin and culminating in a closed heath formation, complicated at almost all stages by the retarding or diverting effects of fresh- or salt-water flooding and by the secondary invasion of blown sand. The general result is to give an extremely complex mosaic of successional vegetation states.

There remains to be noticed one factor tending to obscure the simplified vegetation picture just given, the presence of certain scattered areas which still show the effects of former human activities. These are the old enclosures (which represent attempts, now nearly all long abandoned, to cultivate, or at least utilise, parts of the peninsula) and the woods, which certainly owe some of their present character to human agency. The total area of these modified

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areas is small, but they are often of interest as illustrating a series of stages in retrogression to a natural condition.

The following detailed description of the vegetation is arranged according to the three basic categories described above. The harbour shore is, in accordance with its peculiar nature, considered first. Then the Western Plateau is described and the complicated Eastern Sands come last. The various modified habitats are included as appropriate.

THE HARBOUR SHORE.

(Plate XXIII, 1 and 2.)

In striking contrast to Studland Bay the shore on the harbour side of the peninsula is very narrow, the width very rarely exceeding 20 yards. The inward or landward part of the shore is predominantly gravelly or sandy, being formed from the debris from the plateau above. Beyond this the shore is in varying degrees muddy owing to the mixture of harbour silt. Again, beyond this and outside the shore proper is a wide expanse of unmixed harbour mud. Until this century the mud was almost uncolonised by vegetation, but in 1899 a few plants of *Spartina Townsendi* were discovered a few miles farther west of South Haven Peninsula. Thence it has since spread with great rapidity in all directions until to-day enormous areas of mud are covered with it and it has become by far the most conspicuous feature in the vegetation of the harbour. At South Haven although abundant it is not at its best. Its greatest development is towards the west end of the harbour where the salinity is less.¹

The vegetation of the harbour shore closely follows the zonation of the substrate. The landward zone under the low plateau cliffs is beyond the reach of all but exceptional tides, but is generally somewhat damp owing to minor drainage from above. Here the vegetation is very mixed, including stragglers from the adjacent heathland and, where local fresh-water drainage is marked, such hygrophilous species as *Hydrocotyle vulgaris*, *Lycopus europaeus* and *Carex binervis*, but the bulk of the vegetation consists of species characteristic (at least in this part of Dorset) of damp sandy, and often slightly saline, habitats. Conspicuous among these are:

Alchemilla arvensis	E. pulchella	Polygonum aviculare
Anagallis arvensis	Juncus articulatus	Potentilla Anserina
-- Carex extensa	Leontodon taraxacoides (hirtum)	--Radiola linoides
--Centunculus minimus	Matricaria inodora	--Samolus Valerandi
Cerastium tetrandrum	--Oenanthe Lachenalii	Scirpus setaceus
Erythraea Centaurium	Plantago Coronopus	Spergula vulgaris

The outer zone of the shore proper bears a well-marked mixed salt-marsh vegetation in which the principal species are:

Armeria maritima	J. Gerardi	Spergularia marginata
Atriplex portulacoides	Plantago maritima	Statice Limonium
Glaux maritima	Salicornia appressa	Suaeda maritima
Glyceria maritima	S. ramossissima	Triglochin maritimum
Juncus maritimus	Spartina Townsendi	

¹ Oliver, F. W. "*Spartina Townsendi*: its mode of establishment, economic uses and taxonomic status." This JOURN. 13, 74-91, 1925.



Phot. 1. The head of Bramble Bush Bay, looking south from the end of Gravel Spit. *Spartina*, *Salix*, *Glauca* and *Suaeda* on the shore. Edge of Western Plateau in the background.



Phot. 3. Interior of 12-acre Wood in the wetter part. Large clump of *Osmunda* in right foreground, others in middle distance. Buckles birches and willows.



Phot. 2. Redhorn Bay, looking north. *Spartina* in the harbour water: large patches of *Juncus maritimus* in foreground. Redhorn Quay in the distance.



Phot. 4. Northern part of Plateau Enclosure, looking north. Third Ridge in background.

The degree of development of this fringing salt marsh varies considerably according to the physical character of the shore. In the north, where the shore becomes increasingly sandy, it disappears, and it is poor where there is much gravel and little mud.

At two points on the shore the vegetation is quite different from the above. At Sandy Point, which separates Plateau and Dyke Bays, there is a small mobile sand-dune strongly colonised by *Psamma* and some of the usual associates (see pp. 388, 389 below). This is the only dune west of the Eastern Sand, and its occurrence here right in the middle of the harbour shoreline is not readily explained. At the junction of Plateau and Redhorn Bays there is a small raised artificial promontory (Redhorn Quay). It was built probably as a quay at which to unload boats bringing building materials for the construction of Redhorn Cottage which formerly stood in Plateau Enclosure. It has long been derelict and now bears a short dry turf. In this turf and on the lower slopes and neck of the quay the flora is rich, including several species rare or absent elsewhere on the peninsula. Many of these are normally calcicolous plants, and it is presumably the presence of such substances in the extraneous matter of which the quay is built that accounts for their presence. Among them are:

<i>Atriplex littoralis</i>	<i>Plantago lanceolata</i>
<i>Bellis perennis</i>	<i>Ranunculus Ficaria</i>
<i>Caucalis nodosa</i>	<i>Sedum acre</i>
<i>Cnicus arvensis</i>	<i>Stellaria Boraeana</i>
<i>C. lanceolatus</i>	<i>Thymus Serpyllum</i>
<i>Geranium molle</i>	<i>Trisetum flavescens</i>
<i>Hyoscyamus niger</i>	<i>Vicia lathyroides</i>
(1 plant in 1932; 5 in 1933)	

The zonation of species on the harbour shore.

One of the most interesting features of the shore vegetation is the zonation shown by many of the species. This, owing to the narrowness of the shore and the number of species on it, is often very detailed although it varies considerably from place to place. The following four examples, taken at intervals between Brand's Creek and South Haven Point, illustrate this well.

No. 1. In Brand's Creek. Total width of shore about 15 yards.

Zone 1 (outermost). *Spartina*, with *Statice*, *Salicornia* and *Triglochin maritimum*.

Zone 2. *Juncus maritimus*, with

<i>Armeria maritima</i>	<i>Suaeda maritima</i>
<i>Glaux maritima</i>	<i>Triglochin maritimum</i>
<i>Samolus Valerandi</i>	<i>T. palustre</i>
<i>Spergularia marginata</i>	

Zone 3. *Juncus maritimus*, with

<i>Agrostis tenuis</i>	<i>Juncus effusus</i>
<i>Carex distans</i>	<i>J. Gerardi</i>
<i>C. extensa</i>	<i>Leontodon taraxacoides</i> (hirtum)
<i>Centunculus minimus</i>	<i>Lotus corniculatus</i>
<i>Erythraea Centaurium</i>	<i>Oenanthe Lachenalii</i>
<i>E. pulchella</i>	<i>Plantago maritima</i>
<i>Festuca rubra</i>	<i>Potentilla Anserina</i>
<i>Glaux maritima</i>	<i>Schoenus nigricans</i>
<i>Holcus lanatus</i>	<i>Trifolium repens</i>
<i>Hydrocotyle vulgaris</i>	

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Zone. 4. A mixture of

Agropyron pungens
 Alchemilla arvensis
 Anagallis arvensis
 A. tenella
 Cerastium semidecandrum
 C. tetrandrum
 C. vulgatum
 Erica cinerea
 Erythraea Centaurium
 E. pulchella

Jasione montana
 Polygonum aviculare
 Potentilla Anserina
 Rumex Acetosella
 R. crispus
 Rubus
 Sagina procumbens
 Sedum anglicum
 Teucrium Scorodonia
 Ulex europaeus

No. 2. *In Plateau Bay.*

Zone 1 (outermost). A very broad belt of *Spartina* with some *Zostera nana*.

Zone 2. *Armeria maritima*
Glyceria maritima
Salicornia appressa

Salicornia ramossissima
Spergularia marginata
Statice Limonium

Zone 3. *Agrostis tenuis*
Erythraea Centaurium
Festuca rubra
Hydrocotyle vulgaris
Juncus conglomeratus
J. effusus
J. maritimus
Leontodon taraxacoides (hirtum)

Plantago Coronopus
P. maritima
Potentilla Anserina
Rosa rubiginosa (occ.)
Rumex crispus
Sedum anglicum
Solanum Dulcamara

No. 3. *In Dyke Bay.*

Zone 1 (outermost). *Spartina*.

Zone 2. *Statice Limonium*.

Zone 3. *Armeria maritima* and *Spergularia marginata*.

Line of tidal refuse.

Zone 4. *Plantago maritima* and *Juncus Gerardi*.

Zone 5. *Glaux maritima*.

Zone 6. *Agrostis alba*
Anagallis tenella etc.

Plantago Coronopus
Radiola linoides

Zone 7. *Hydrocotyle vulgaris*
Juncus effusus etc.

Potentilla Anserina

No. 4. *Jerry's Point.*

This promontory ends in a very conspicuous and strongly hooked gravelly point in association with which there is the following peculiar and interesting vegetational zonation:

Zone 1 (outermost). The harbour mud and silt surrounding the hook is colonised by *Spartina*, mostly pure but in the angle of the hook accompanied by *Statice Limonium*.

Zone 2. The lower slopes of the neck and north side of the hook are covered with a turf containing:

Atriplex portulacoides
Glyceria maritima
Lepturus filiformis

Spergularia marginata
Statice Limonium
Suaeda maritima

Zone 3. The lower slopes on the east and south sides of the hook have a similar turf of:

Armeria maritima
Lepturus filiformis
Plantago maritima

Salicornia appressa
S. ramossissima
Spergularia marginata

Zone 4. The higher central part of the hook has the following species:

Agropyron pungens
Agrostis alba
Armeria maritima
Atriplex hastata
A. portulacoides
Beta maritima
Cerastium tetrandrum
Cochlearia anglica
Festuca ovina
F. rubra

Glaux maritima
Juncus Gerardi
Lepturus filiformis
Plantago Coronopus
P. maritima
Polygonum aviculare
Sagina ciliata
S. procumbens
Spergularia marginata
Triglochin maritimum

THE WESTERN PLATEAU.

As mentioned already, the natural plant covering of the plateau is heath, this being the type of vegetation characteristic of the podsolised soils derived from the Bagshot deposits of southern England. The dominant species are *Calluna*, *Erica cinerea* and *E. Tetralix*, together with a varying mixture of *Pteris*. This vegetation is found all over the more elevated parts of the plateau except where the influence of man has made itself felt, as for instance in the enclosures, the woods, and the shrubbery round the ruins of Curlew Cottages. In the valleys or where soil drainage is impeded the heath is replaced by progressively damper communities, culminating either in acid bog or in swamp. Throughout the plateau, and indeed throughout the peninsula, *Pinus sylvestris* and, very occasionally, *P. Pinaster*, occur thinly and subspontaneously.

Heath.

For general convenience the heaths of the plateau have been divided into several distinct topographical parts, but this segregation has little or no botanical significance and the vegetation is practically constant throughout.

The most widespread, and generally most plentiful, species are:

<i>Agrostis setacea</i>	<i>Polygala serpyllacea</i>
<i>Calluna vulgaris</i>	<i>Pteris aquilina</i>
<i>Cuscuta Epithymum</i>	<i>Scirpus caespitosus</i>
<i>Erica cinerea</i>	<i>Ulex europaeus</i>
<i>E. Tetralix</i>	<i>U. minor</i>
<i>Molinia coerulea</i>	

The two grasses are relatively sparse and the vegetation as a whole has a slightly damp facies. Where conditions tend to be unusually dry other species also occur. Many of these are casuals but among the more general are:

<i>Anthoxanthum odoratum</i>	<i>Potentilla erecta</i>
<i>Betula alba</i> , mostly as seedlings	<i>Rubus</i> spp.
<i>Cardamine hirsuta</i>	<i>Scabiosa Succisa</i>
<i>Leontodon taraxacoides</i> (hirtum)	<i>Scilla non-scripta</i>
<i>Myosotis collina</i>	

Conversely where conditions become wetter the following appear:

<i>Carex panicea</i>	<i>Juncus sylvaticus</i> (acutiflorus)
<i>Drosera longifolia</i>	<i>Pedicularis sylvatica</i>
<i>D. rotundifolia</i>	<i>Salix repens</i>

Rarely do many of these species occur together, and the local communities are very poor in species. Over much of Plateau Heath and Brand's Heath, for instance, the only plants are the three ericoids and *Ulex minor*, with a slight mixture of *Molinia* and *Agrostis*. The most conspicuous variation from the normal is on the slopes immediately south-east of Curlew Cottages, where *Agrostis setacea* is very abundant.

Along the edge of the plateau, where it borders the harbour, there is a marked belt of *Ulex europaeus* with such plants as *Rubus* spp. and *Rosa*, together with large *Pteris*, *Lonicera* and *Scilla*. The same type of community is even better developed on the eastern part of Western Arm Heath and in the adjacent Little Sea Enclosure. Here *Pteris* and *Ulex* are very dense and dominant and accompanied by occasional *Betula*, *Salix cinerea* and *Sorbus aucuparia*.

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To facilitate future comparisons it is worth while giving the present (1932) distribution of *Pteris* in some detail. On Wood Heath and Pipleigh Heath it is fairly general and well developed, but not of any great size. On Western Arm Heath it is confined to the eastern peninsula, but here and in Little Sea Enclosure it is very large and dense. On Curlew Heath it is general east of the old track, that is to say along the edge of Little Sea. Over Spur Heath it is general except roughly within the 50-ft. contour line, and in the north tends to be very dense. On Brand's Heath it occurs rather thinly on the southern part and more densely along the harbour edge. On Plateau Heath similarly it bounds the edge but inland is very variable, in some places being continuous though small, and elsewhere absent.

A conspicuous feature in the vegetation of Plateau Heath is a series of shallow circular depressions said to have been dug out some forty years ago as drinking pools for duck, presumably when the water of Little Sea was still saline. They are now more or less overgrown and without standing water. They number fifteen, and in the ten examined the following species occurred:

<i>Molinia coerulea</i>	10	<i>Potentilla erecta</i>	3
<i>Carex panicea</i>	9	<i>Hydrocotyle vulgaris</i>	3
<i>Eleocharis palustris</i>	8	<i>Juncus supinus</i>	2
<i>Salix repens</i>	4	<i>Carex Goodenowii</i>	1

The numbers show the number of pools out of the ten observed in which each occurs. *Sphagnum* is present in all and there is commonly a marked edging of *Erica Tetralix*.

Bog and swamp.

At three spots on the Western Plateau acid bog with much *Sphagnum* is well developed, i.e. in Spur Bog, on the extreme south-western slope of Brand's Heath, and in Wood Marsh. The only difference between the first two is that the second is smaller and less rich in species and tends to dry out completely in a dry season. The third, although having many species in common with the others, has a very distinct appearance owing to the greater development of larger and coarser plants, and to its more sheltered position. It is thus of rather different ecological value, especially as an animal habitat.

Spur Bog is an excellent example of the valley bogs so common on the heathlands of Dorset and Hampshire, and it is therefore worth giving its flora in detail:

<i>Agrostis</i> sp.	<i>Lycopodium inundatum</i>
<i>b</i> <i>Calluna vulgaris</i>	<i>b</i> <i>Molinia coerulea</i>
<i>b</i> <i>Carex panicea</i>	<i>b</i> <i>Myrica Gale</i>
<i>Drosera anglica</i>	<i>b</i> <i>Narthecium ossifragum</i>
<i>D. longifolia</i>	<i>Orchis Fuchsii</i>
<i>b</i> <i>D. rotundifolia</i>	<i>b</i> <i>Pedicularis sylvatica</i>
<i>Eleocharis multicaulis</i>	<i>b</i> <i>Pinguicula lusitanica</i>
<i>b</i> <i>Erica Tetralix</i>	<i>b</i> <i>Polygala serpyllacea</i>
<i>b</i> <i>Eriophorum angustifolium</i>	<i>Potamogeton polygonifolius</i>
<i>Gentiana Pneumonanthe</i>	<i>b</i> <i>Potentilla erecta</i>
<i>Holcus lanatus</i>	<i>b</i> <i>Rhynchospora alba</i>
<i>b</i> <i>Juncus bulbosus</i>	<i>b</i> <i>R. fusca</i>
<i>J. sylvaticus (acutiflorus)</i>	<i>b</i> <i>Scirpus caespitosus</i>
<i>b</i> <i>Lotus uliginosus</i>	

The species marked *b* above are found also in Wood Marsh and this locality has in addition:

Hydrocotyle vulgaris
Osmunda regalis
Phragmites communis

Pteris aquilina
Salix cinerea

Comparisons with similar valleys elsewhere in the neighbourhood suggest that the area now known as Piplely Swamp was also originally the bottom part of an acid valley bog, perhaps of the kind seen in Wood Marsh. The rise of Little Sea, however, presumably drowned out the existing vegetation, and to-day it consists of an open reed swamp of *Phragmites*, in which are many bushes of *Salix cinerea* and, towards the edges, *Betula alba*. Seen from a little distance the sallow and birch are very conspicuous. Among these three dominant species occur many others of which the following are the most important:

Blechnum Spicant
Cnicus pratensis
Eleocharis palustris
Hypericum elodes
Galium palustre
Juncus effusus
J. sylvaticus (acutiflorus)
Lotus uliginosus
Mentha aquatica

Menyanthes trifoliata
Molinia coerulea
Myrica Gale
Orchis Fuchsii
Osmunda regalis
Potamogeton polygonifolius
Ranunculus Flammula
Scutellaria minor

Old enclosures.

(Plate XXIII, 4.)

Plateau Enclosure first appears on the map of 1849 and a cottage, which has now almost entirely disappeared, is shown within it. This cottage was called Redhorn, and it may well be that Redhorn Quay was constructed when it was built. The enclosure continued latterly to be used as a garden by the keepers living on the peninsula until the war, and its present retrogressive vegetation dates from about 1914.

The bulk of the vegetation to-day consists of a dense thicket of *Pteris*, *Rosa rubiginosa*, *Rubus*, *Ulex europaeus*, *Erica cinerea* and *Salix cinerea*. The first two species predominate in the southern part and the third in the northern. Especially in the north there are wide open areas of short damp turf and the larger part of the enclosure is covered by a layer of blown sand.

Piplely Enclosure similarly is largely covered with blown sand. It first appears as an enclosure in the 1811 map, by which date the building shown in Avery's early survey had disappeared. Its natural condition has certainly been modified to some extent in the past, but how much is not certain. Little evidence of this is now left, and I am informed that it has not been cultivated within living memory.

Its vegetation is now for the most part a dense *Pteris* cover with many scattered bushes, passing in the north-east into open thicket. Here and there are open patches of sandy turf, but these are not considerable. In places, particularly on the edges, the enclosure is very damp.

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The species lists of these two enclosures are long—in Plateau about seventy have been noted and in Pipley about ninety. Some forty of these are common to both, and include such species, common on grassy heaths, as the ericoids, *Scilla non-scripta*, *Viola Riviniana* and *Teucrium Scorodonia*. There are also many species characteristic often of cultivated places, such as *Achillea Millefolium*, *Bellis perennis*, *Cynosurus cristatus*, *Plantago lanceolata*, *Ranunculus repens*, *Trifolium repens* and *Urtica dioica*.

Among the thirty species found only in Plateau quite half are characteristic of damp sandy places (see *infra*), as, for instance, *Montia fontana*, *Radiola linoides*, *Scirpus setaceus*, and *Trigonella ornithopodioides*. The rest are nearly all common plants often associated with some form of cultivation.

The fifty in Pipley only include a dozen hygrophilous species, such as *Lycopus* and *Spiraea Ulmaria* from the damper edges, and a small group of hedge or woodland species, e.g. *Ajuga reptans*, *Conopodium majus*, *Galium Cruciatum*, *Primula veris* and *P. vulgaris*, *Ranunculus Ficaria*, and *Tamus*. Among the rest *Campanula rotundifolia*, *Carex praecox*, *Euphrasia*, *Hypericum pulchrum* and *Rosa spinosissima* are, elsewhere in the peninsula, rare or entirely absent.

Woods.

(Plate XXIII, 3.)

Three woods, namely 12-acre, 3-acre and Aspen, are shown on the map, but from a botanical point of view the first two of these may be treated as one under the name Southern Wood. They lie west of Little Sea and are therefore, except for a little blown sand, on the Tertiaries. Aspen Wood, on the other hand, is perhaps entirely east of the former edge of the Tertiaries, but the actual line of demarcation is very difficult to follow, owing to the masking by the superficial blown sand.

Southern Wood appears to have had a long history. Trees are shown here in Avery's time, and if this evidence is to be relied on there was woodland here at the beginning of the eighteenth century. The subsequent maps are not easy to interpret in this connection, but it is my opinion that, despite fluctuations in extent, there has always been some woodland in this part of the peninsula since that date. This is supported by the statement made to me that until a few years ago there were, in the vicinity, three very large elm trees. These may well have been the immediate descendants or even an actual part of Avery's wood. At all events it would seem that a woodland habitat has persisted hereabouts for more than 250 years at least.

At present birch and willow are the dominant trees of the wood, and the former is especially abundant and large, reaching a height of 40 ft. and a trunk diameter indicating considerable age. In the thinner western part of the wood are several isolated individuals of species such as oak, elm and yew, which are not found in the denser eastern parts, and these may be the remains

of earlier woodland. In the south-eastern part there is a good deal of hazel which was planted about 40 years ago and which is periodically coppiced. In places the wood is wet and is here remarkable for the great development of *Osmunda regalis* and *Juncus* spp., the former reaching a height of 6 ft.

The Aspen Wood (practically a pure stand of *Populus tremula*) is, I am informed on what seems to be good authority, a natural wood in which the oldest trees, some 25 ft. high, are about 35 years old. It is spreading, at least towards the west, by suckers, and most of the trees are now fertile. Its occurrence is of considerable interest, since this species is, other than individually, rare in the neighbourhood and on the peninsula there are only one or two other small plants.

The following is a tabulated list of the species which have been recorded from the two woods. It should be remembered that Aspen Wood is much smaller than Southern Wood.

	Southern Wood	Aspen Wood		Southern Wood	Aspen Wood
<i>Agrostis tenuis</i>	x	x	<i>Luzula campestris</i>	x	.
<i>Ajuga reptans</i>	x	x	<i>Molinia coerulea</i>	x	.
<i>Anagallis tenella</i>	.	x	<i>Nepeta hederacea</i>	x	.
<i>Anthoxanthum odoratum</i>	x	.	<i>Osmunda regalis</i>	x	.
<i>Arenaria trinervia</i>	x	.	<i>Poa trivialis</i>	x	.
<i>Athyrium Filix-foemina</i>	x	.	<i>Populus tremula</i>	.	x
<i>Bellis perennis</i>	x	x	<i>Potamogeton polygonifolius</i>	.	x
<i>Betula alba</i>	x	.	<i>Potentilla erecta</i>	x	x
<i>Blechnum Spicant</i>	x	.	<i>P. sterilis</i>	x	x
<i>Cardamine pratensis</i>	.	x	<i>Primula vulgaris</i>	x	x
<i>Carex binervis</i>	x	.	<i>Prunella vulgaris</i>	x	x
<i>C. echinata</i>	x	.	<i>Prunus spinosa</i>	x	x
<i>C. Goodenowii</i>	x	.	<i>Pteris aquilina</i>	x	x
<i>Cnicus palustris</i>	x	x	<i>Pyrus Malus</i>	x	.
<i>Conopodium majus</i>	x	x	<i>Quercus Robur</i>	x	.
<i>Corylus Avellana</i>	x	.	<i>Ranunculus Ficaria</i>	x	x
<i>Crataegus monogyna</i>	x	x	<i>R. Flammula</i>	x	.
<i>Epilobium palustre</i>	.	x	<i>R. repens</i>	x	x
<i>E. tetragonum</i>	x	.	<i>Rosa canina</i>	.	x
<i>Erica Tetralix</i>	x	.	<i>Rubus sp.</i>	x	x
<i>Fragaria vesca</i>	x	x	<i>Rumex Acetosa</i>	x	.
<i>Galium Aparine</i>	x	x	<i>Salix aurita</i>	x	.
<i>G. palustre</i>	x	x	<i>S. cinerea</i>	x	x
<i>G. saxatile</i>	x	.	<i>Sambucus nigra</i>	x	.
<i>Hedera Helix</i>	x	x	<i>Scilla non-scripta</i>	x	x
<i>Holcus lanatus</i>	x	x	<i>Scutellaria minor</i>	x	x
<i>H. mollis</i>	x	.	<i>Solanum Dulcamara</i>	.	x
<i>Hydrocotyle vulgaris</i>	x	x	<i>Sorbus aucuparia</i>	x	.
<i>Ilex Aquifolium</i>	x	x	<i>Tamus communis</i>	x	x
<i>Juncus sylvaticus (acutiflorus)</i>	x	x	<i>Taxus baccata</i>	x	.
<i>J. bulbosus</i>	x	.	<i>Teucrium Scorodonia</i>	x	x
<i>J. conglomeratus</i>	x	x	<i>Ulex europaeus</i>	x	.
<i>J. effusus</i>	x	x	<i>Ulmus montana</i>	x	.
<i>J. subnodulosus (obtusiflorus)</i>	x	.	<i>Urtica dioica</i>	x	.
<i>Lastrea aristata</i>	x	x	<i>Veronica Chamacdrys</i>	x	x
<i>L. Filix-mas</i>	.	x	<i>V. officinalis</i>	x	.
<i>Listera ovata</i>	x	x	<i>Viola Riviniana</i>	x	x
<i>Lonicera Periclymenum</i>	x	x	<i>V. silvestris</i>	x	.
<i>Lotus uliginosus</i>	x	x			

The new road.

The construction of the new motor road from Pipley to South Haven some years ago has had a twofold effect on the vegetation of the peninsula. Not only did it result in a series of new viatical habitats but the importation of road materials provided that small amount of calcareous matter which permitted the entry into these new habitats of certain species hitherto absent from the peninsula. As a result of this the present flora of the artificial road margins and their immediate vicinity is rich and varied. No fewer than eighty species have so far been noted from them, and of these the following, some of which are calcicolous, occur practically nowhere else on the peninsula:

Bartsia Odontites
Blackstonia perfoliata
Clinopodium vulgare
Carex divulsa
Daucus Carota
Deschampsia caespitosa
Eupatorium cannabinum
Juncus inflexus

Linum catharticum
Medicago lupulina
Ononis repens
Pastinaca sativa
Plantago major
Potentilla procumbens
Rumex obtusifolius

The effect of the introduction of road materials either from other parts of the area or from outside is seen very vividly about half a mile north of Pipley Bridge, where the road traverses the western extremity of Spur Bog. Here an unusually large amount of material has gone to form the road foundations. Some of it has become washed down towards and into the bog, and as a result there is in the part of the latter immediately adjoining the road, the following extraordinary mixture of species, some viatical, some calcicolous, some bog and some even saline:

Arctium minus
Blackstonia perfoliata
Carex Goodenowii
C. leporina
C. panicea
Cerastium vulgatum
Eleocharis multicaulis
Equisetum arvense
Erica Tetralix
Eriophorum angustifolium
Erophila verna
Erythraea Centaurium
Festuca rubra
Gentiana Pneumonanthe
Holcus lanatus
Juncus articulatus (lampocarpus)
J. effusus

J. maritimus
J. sylvaticus (acutiflorus)
Leontodon taraxacoides (hirtum)
Linum catharticum
Lotus uliginosus
Luzula campestris
Molinia coerulea
Pedicularis sylvatica
Prunella vulgaris
Pulicaria dysenterica
Sagina procumbens
Salix cinerea
Schoenus nigricans
Scilla non-scripta
Scirpus caespitosus
Ulex minor

Finally, in connection with the motor road mention must be made of a peculiar area south of Pipley Bridge and adjoining the road on the east. This is an open stretch of damp sandy gravel formed partly by the road-making operations but comprising also the present bridle and foot entrance to Pipley Enclosure. To it there has been given, since the publication of Diver's map, the name Pipley Road Waste. It bears a rich flora including many viatical species, one or two of which are not found elsewhere but is of particular interest

because of the number of species on it which elsewhere on the peninsula are characteristic on one hand of the inner zone of the Harbour Shore (see *supra*) and, on the other, of the damp sandy areas of the Eastern Sands (see *infra*). These species and certain others worthy of note are as follows:

<i>Carex flava</i>	<i>Microcala filiformis</i>
<i>Centunculus minimus</i>	<i>Nardus stricta</i>
<i>Erythraea Centaurium</i>	<i>Pedicularis sylvatica</i>
<i>E. pulchella</i>	<i>Plantago Coronopus</i>
<i>Hypericum humifusum</i>	<i>Pulicaria dysenterica</i>
<i>Juncus bufonius</i>	<i>Radiola linoides</i>
<i>J. effusus</i>	<i>Sagina procumbens</i>
<i>J. inflexus</i>	<i>Salix repens</i>
<i>J. articulatus (lampocarpus)</i>	<i>Scrophularia aquatica</i>
<i>J. sylvaticus (acutiflorus)</i>	<i>Veronica serpyllifolia</i>

THE EASTERN SANDS.

History.

It is necessary for the proper understanding of the interrelationships of the different types of habitat and vegetation now existing in this part of the peninsula to repeat here much that has already been said elsewhere concerning its history.

In the seventeenth century, as for an unknown length of time previously, the eastern shore of the peninsula closely followed the eastern edge of what is now the Western Plateau, but towards the end of that century an accretion of sand commenced along this line. The shoreline was, however, not straight but slightly concave, and the initial ridge of drifted sand took the line of a chord across this curvature, leaving on the west side of the ridge an appreciably wide and level zone in the centre of the chord. This area became eventually the bed of Little Sea. But there flowed into this shallow bight the drainage of the plateau at three distinct points, and this was apparently sufficient to prevent the formation of a single continuous sand ridge along the whole length of the chord. As a result the ridge was laid down in two separate parts, a northern and a southern, each based on an extremity of the plateau and leaving a gap between the halves by which the drainage water from the land found an exit to the sea.

Two further ridges were subsequently deposited in much the same way but with two important differences. In each ridge the central gap was smaller than that of the preceding ridge, and while in the south the ridges were more or less superimposed, in the north they were separated by considerable slacks or level valleys. As a result of this progressive narrowing of the central gap the escape of the water which began to accumulate in what is now Little Sea became more and more impeded until, with the final and comparatively recent closing of the gap in what is now known as First Ridge it became entirely prevented.

This final completion of the dune line was the crucial point in the development of the area, since it resulted in a much accelerated accumulation of land drainage water within it. The former line of escape being now closed, the only way by which the water could reach the sea was by one or both of the two main slacks between the northern parts of the three ridges, but before this could take place the level of the water had necessarily to rise considerably. It was in this process that Little Sea as an enclosed sheet of water came into being.

Had the accumulation of this water been allowed to continue until it could escape naturally, Little Sea would have deepened till it overflowed down either or both of the two slacks, but before this could occur an artificial outlet was provided by the making of Central Cut between Third Ridge and Second Ridge and the level of Little Sea became thereby more or less stabilised. Not altogether so, because water still accumulated afterwards, though much more slowly, until in 1932, when this survey was begun, there were, in addition to Little Sea proper, the body of water known as Eastern Lake and the waterlogged area known as East Marsh, both resulting from the local overflowing of Little Sea itself.

The primary factor in the formation of Eastern Sands has been the continuous deposition of sand during the last 250 years. If this had not been interfered with in any way it would have led, gradually, to an increasing stabilisation with a slow but persistent passage, as regards plant habitats, from a wet to a dry condition. The slow elevation of the area as a whole would gradually have neutralised or overcome the influence of tidal water until the whole system would have become more and more actually dry sand. No doubt this would have been a lengthy process, locally impeded by such factors as rainfall, but the ultimate effect would have been inevitable.

Owing, however, to the simultaneous accumulation of drainage water as a secondary effect of the sand accretion the case was radically altered. The simple process of stabilisation just outlined continued for a while, but comparatively soon this secondary factor made itself felt. From this time onward any progressive drying out of the area as a whole was more than counterbalanced by the failure of drainage water to escape. Thus there was early initiated a second sequence of events which, from the point of view of plant development, tended to neutralise, and locally even to reverse, the more fundamental primary process.

A further complication also came into play. The gradual and normal drying out of the sands was a process involving the elimination of saline water, but the increase of Little Sea was an augmentation of fresh water. Hence the change was not merely a straightforward reversal but the replacement of one process by an opposite process of a rather different kind. This unusual combination of events and circumstances is the reason why South Haven Peninsula is of particular biological interest and importance and why it has developed an unusual range and complexity of habitats.

Expressed shortly, the vegetation of the Eastern Sands to-day exhibits a plexus of developmental conditions resulting from the interaction of four distinct factors, i.e. dryness of soil, wetness of soil, salinity of soil water and freshness of soil water. In these circumstances the richness of the flora is not surprising. While two of these factors, dryness and wetness of substratum, are more or less antagonistic, their combined effect has been to increase the rapidity with which the soil loses salinity, and this feature doubtless accounts for the great speed with which the vegetation of some localities has reached a comparatively high state of development.

How far the damming up of Little Sea has affected the absolute water content of the soil in outlying parts of the area is difficult to determine, but considering the porous nature of the sand it would seem that its effect must be considerable and that the damp and wet vegetation facies in many places must be due, partly at least, to this factor rather than to the retention of the original saline water. Certainly it appears that, except for the newest dunes, the whole area is less dry than it used to be.

Finally there must be mentioned the rapid changes which have taken place in Shell Bay in recent years, during which time the shoreline has undergone great alteration. In 1894, for instance, the shore was, at its central point, 200 yards farther north than it is now. Correlated with this is the fact that the present shore-edge dunes in this part are among the newest sand accretions.

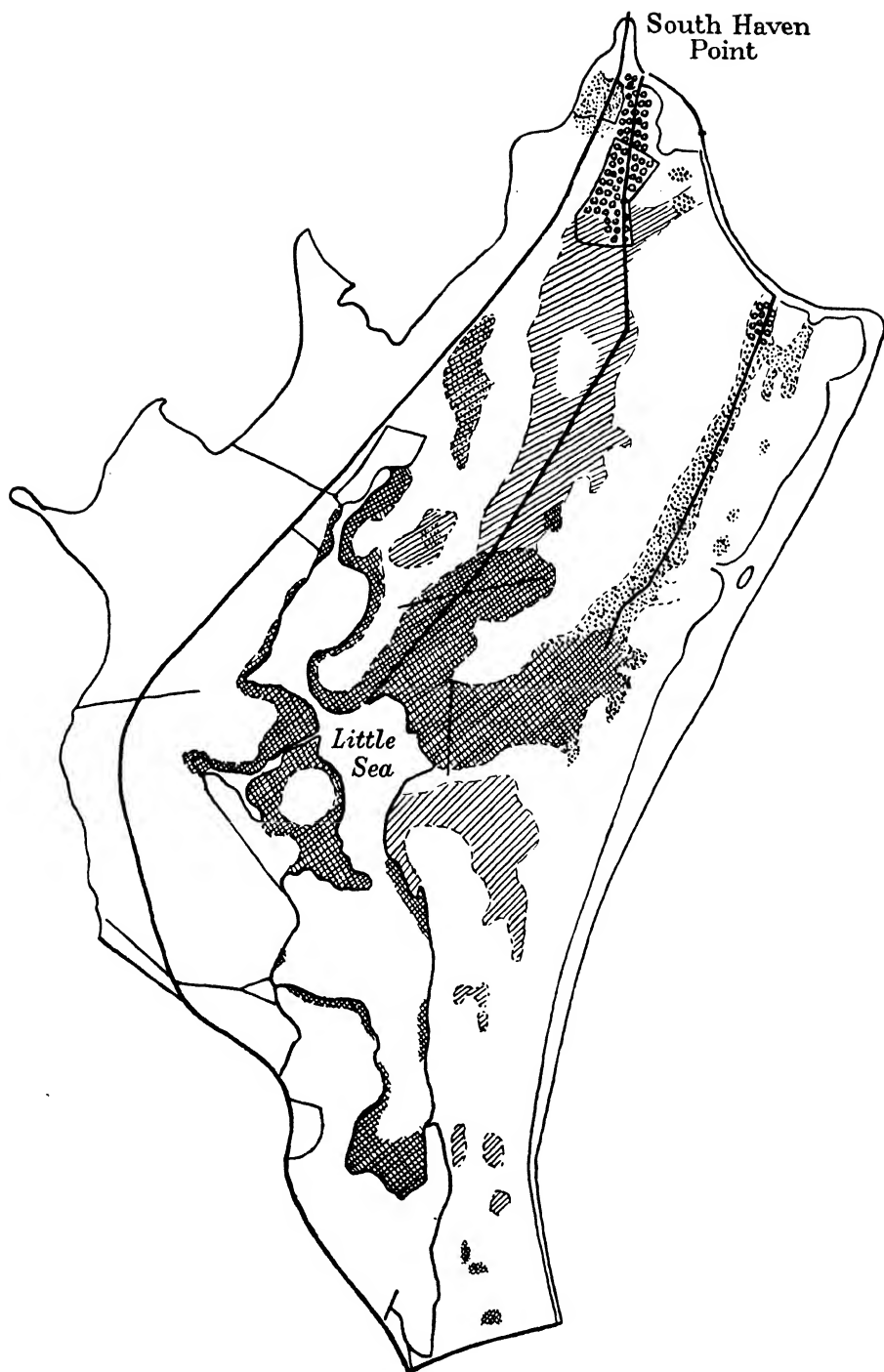
The total effects of the processes described above have been to produce a wide range of plant habitats each supporting a more or less characteristic flora. At the same time so many intermediate conditions occur that it is almost impossible to describe the whole in detail, and any classification must be, to some extent, arbitrary. The main object in the following pages is, therefore, to give as complete an account of the vegetation as is practicable, bearing in mind that the chief value of such an account must be to provide a foundation upon which future studies and comparisons can be based. To do this some simplification in presentation has been essential. First there is given a short general account of the main habitat and vegetation series. This is followed by more detailed descriptions of these together with such historical information as appears relevant, and, when necessary, lists of specially interesting plant communities. Unless otherwise stated it may be assumed that the state of affairs described is that existing in the summers of 1932 and 1933.

General description of the vegetation.

The basic consideration in the classification of the vegetation types of the Eastern Sands is that the building up of the area has resulted in a series of sand ridges separated to a varying extent by level low-lying slacks. In other words, a series of almost inevitably dry habitats alternates with a series of potentially wet habitats, and, owing to the accumulation of water behind the ridges, this potentiality has become a fact. Thus there are primarily two vege-



MAR 2. Sketch-map showing the approximate distribution, on Eastern Sands in 1932-33, of the following types of vegetation: Dune-Grass, stipple; Dune-Gorse, circles; Dune-Heath, line and stipple; Dry Heath, line; Pteris-Heath, crossed lines.



MAP 3. Sketch-map showing the approximate distribution, on Eastern Sands in 1932-33, of the following types of vegetation: Damp Sand Communities, stipple; Salt Marsh, circles; Acid Bog, line and stipple; Acid Marsh, line; Swamp, crossed lines.

tation series present. One is a straightforward psammosere of short gamut but slow rate, the other is a reversed hydrosere commencing with saline sand and passing gradually by increase of fresh water to an open aquatic condition. Here then is involved not only a change but to some extent a conflict of soil conditions, and the whole vegetational succession is complex. Besides these two there is evidence also of the beginnings of a third, namely, a normal hydrosere from open fresh water. This is developed only so far as attempts to stabilise the level of Little Sea have had some effect, and is notable only here and in Central Marsh subsequently to the making of Central Cut.

The stages in the psammosere are easily described. In the southern part of Studland Bay there is a fairly continuous zone of strand plants outside the youngest dunes, but this is scarcely a normal stage in the succession and the first real vegetation condition is Dune-Grass dominated by *Psamma* and with a varying amount of *Agropyron*, *Festuca* and other herbaceous associates. Next comes Dune-Heath with *Calluna* and *Erica* as the pioneers and ultimate dominants; and finally there is the edaphic climax, Dry Heath, from which all the dune species have entirely disappeared. This last has two facies according to the presence or absence of *Pteris*. Very locally, owing to land configuration, the amount of water in the soil is increased and the Dry Heath is replaced by a damper type dominated by *Erica Tetralix*. Occasionally the Dune-Heath is replaced by Dune-Gorse in which *Ulex europaeus* almost entirely replaces the ericoids.

The wetter conditions, termed above, for want of a better name, a reversed hydrosere, are much more difficult to describe concisely, chiefly because their beginnings are less definite. Normally the sand levels, after becoming somewhat leached, are colonised by numerous small herbaceous species, including usually some grasses, giving rise to an open turf community. This is very variable in constitution and appearance, but for practical purposes the different kinds are included under the general term "Damp Sand Communities". Locally, however, owing apparently to special conditions of substrate deposition, there is first developed a relatively pure vegetation of *Juncus maritimus* with certain characteristic salt-marsh associates, and this passes either into less saline marsh or into Damp Sand Communities according to subsequent considerations.

The Damp Sand Communities in their turn pass either directly, or through Damp Heath to Acid Marsh, a name used here to comprise those vegetational aspects in which *Molinia*, *Myrica* and *Erica Tetralix* are the co-dominants with *Juncus*, *Carex*, and *Eriophorum* among the more conspicuous associated genera. But this latter vegetation also results from three other changes, namely, the gradual leaching of *Juncus maritimus* marsh; the flooding of heath or dune-heath; and in quite a different way, from the drying out of Swamp (see below). This is the best example of the vegetational convergence which, resulting from the interaction of numerous edaphic factors, is one of the most noteworthy features of the Eastern Sands as a whole.

From the Acid Marsh stage the succession is comparatively simple. In the existing conditions this vegetation is nearly always associated with increased soil water and this, accentuated, leads fairly straightforwardly to swamp conditions, of which there are two variants. In one, true reed-swamp, dominated by *Phragmites*, develops: in the other *Phragmites* is almost or entirely absent and dominance is shared by several species of large *Scirpi* and *Junci*, with *Myrica* important among them. Finally, with accumulation of a considerable depth of standing water, conditions are favourable for the development of a true aquatic community.

Twelve of the main vegetational conditions have been described, leaving three still to be mentioned. The first of these is Acid Bog, that is to say *Sphagnum* bog with such generic associates as *Drosera*, *Hypericum*, *Hydrocotyle* and *Eleocharis*. It has floristic resemblances to both Swamp and Acid Marsh, but develops more or less directly from Heath where there is local stagnation of water in the soil. Over the peninsula as a whole it is seen at its fullest expression in Spur Bog, but on the Eastern Sands it is found only in a small number of isolated pools.

The second type, Sallow-Birch Thicket, is of peculiar interest because of its recent development and because this development indicates the initiation of vegetational changes countering those which resulted from the formation of Little Sea. At present this community is largely found as scattered bushes among the swamp vegetation, but along the edges of Central Marsh, where the valley vegetation meets the foot of the heath-covered ridges, it is specially well developed and forms thickets of considerable size.

Finally there are the communities which owe their constitution to the partial overwhelming of former vegetation by blown sand. These are not widespread and have little mutual relationship, so that they can hardly be incorporated in any general outline. It must, however, be borne in mind that they are theoretically very important as leading to acceleration or retardation of normal succession.

Fig. 1 is an attempt to represent diagrammatically the leading plant associations of the Eastern Sands and to indicate their mutual relationships. A diagram of this kind can only be made reasonably intelligible if it is simplified as much as possible and if somewhat arbitrary decisions are taken as to the appropriate positions of many individual communities. For instance, the term "Damp Sand Communities" has been made to include a number of minor variants, certain of which might, with some show of reason, be included under other headings. Besides this it is desirable to keep the diagram as free from excessive detail as possible, and for this reason two series of data have been omitted from it. These are the factors determining the change from one association to another and the various communities whose presence is due to subsequent local invasions of blown sand. With regard to the first of these the general nature of the habitat changes is to some extent indicated by the

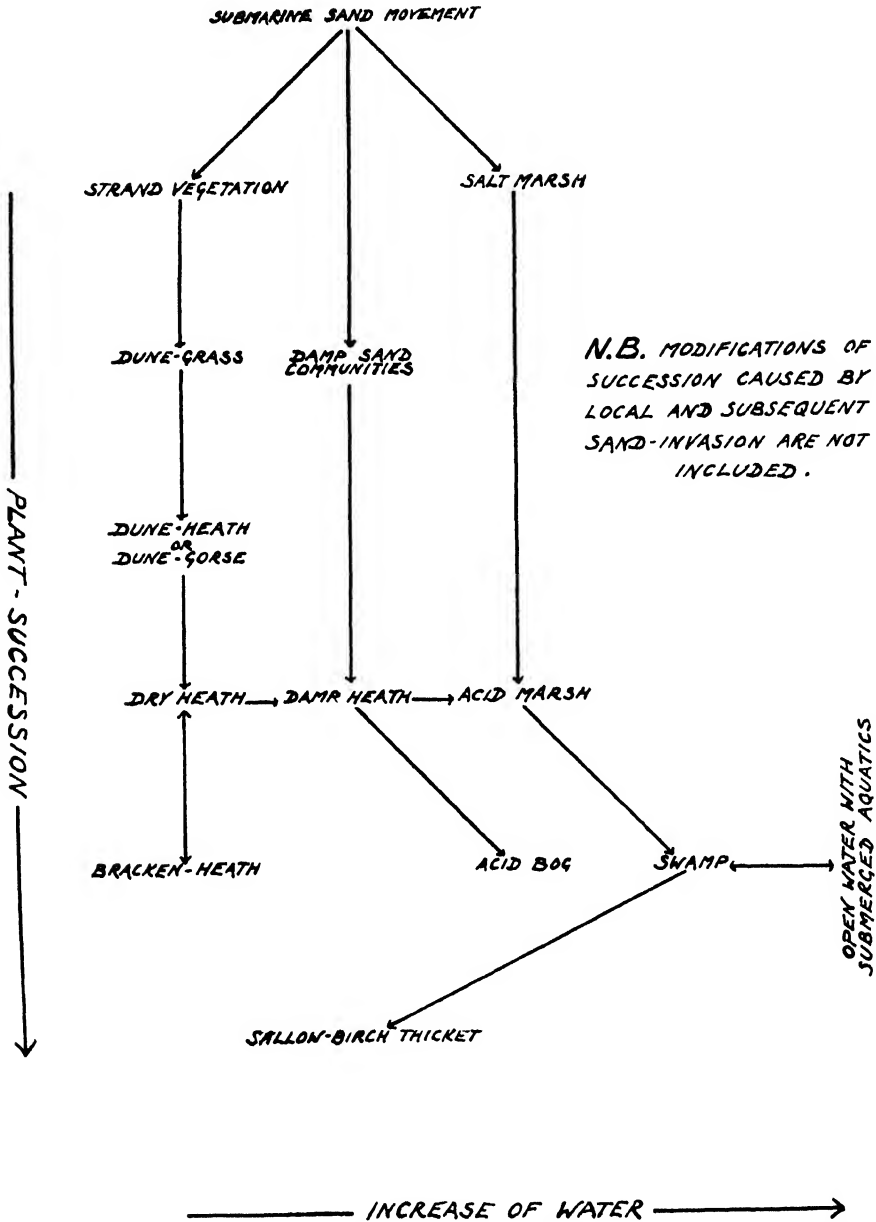


FIG. 1. A diagrammatic representation of the developmental relations between the chief plant-associations of the Eastern Sands, South Haven Peninsula.

arrangement of the diagram in terms of plant succession and water content of the habitat, but further details may appropriately be given here.

The gradual emergence of the blown sand from below sea-level gives rise to three initial plant associations according to the details of the process. If the sand accumulation is rapid, resulting in dunes, the first colonisers are strand plants, very soon giving place to dune-grasses. If, however, the accumulation is gradual and at first intertidal the initial vegetation is Salt Marsh dominated by *Juncus maritimus*. A third condition is found in the "slacks" or levels formed among the dunes and out of direct influence of the tide. Here the first species are some of those characteristic of the Damp Sand Communities, and before long this type of vegetation becomes well developed.

Each of these three initial states is the commencement of a particular series of changes. From the first develops the normal psammose already mentioned, the progressive changes in the habitat being loss of salinity, consolidation of sand and increase of acidity. The result is an oscillation between Heath and Bracken-Heath according to the comparative effect of several factors which are not altogether clear. It will be noticed that an early stage is described as Dune-Heath or Dune-Gorse. The reason for the difference between these two types of vegetation is not at all clear, but it may be that the latter prevails where the substrate is a little damper.

The series commencing with Salt Marsh is a short one, and the vegetation passes almost directly into Acid Marsh by the gradual and fairly rapid replacement of saline water by fresh. This change is a good example of the increased speed of succession where there is secondary accumulation of fresh water.

The third series of changes, from Damp Sand Communities, is also short but is rather more complex than is indicated because of the many slightly different conditions comprised within the term "Damp Sand Vegetation". Here, as in the first series, the factors concerned are consolidation of sand, loss of salinity and increase of acidity.

The various invasion habitats and communities exhibited in the Eastern Sands are described later, but it may be said here that, theoretically at any rate, almost any change from one succession to another is liable to occur if the invasion of sand takes a particular course. Actually those most commonly to be seen are changes to and from the condition of damp sand vegetation.

The vegetation types.

(1) *Strand plants* (Plate XXIV, 5).

The total length of shore from the middle of South Haven Bay to the south-east corner of the peninsula is nearly two miles, but the only part in which there is a conspicuous beach vegetation is in Studland Bay south of Central Gap, and even here the zonation is incomplete. Elsewhere there are only isolated strand plants. In the whole strand vegetation there are only some half a dozen species, namely, *Salsola Kali*, *Atriplex* spp., *Cakile maritima*

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(nearest the dunes), *Arenaria peploides* (nearest the sea), with occasional *Calystegia Soldanella* and *Polygonum Raii*. The incompleteness of the distribution of these strand plants is due to the mobility of much of the shore. They are present only where this is least, as in the southern part of Studland Bay. Here, mingled with the species mentioned, is a good deal of small *Psamma arenaria*, forming the foundation of a new dune line (see Pl. XXIV, phot. 5).

(2) *Dune-Grass* (Plates XXIV-XXVI).

This is the vegetation of the youngest dunes prior to the establishment of ericoid species and occupies a zone of varying width almost throughout the seaward parts of the dunes bordering Shell Bay and Studland Bay. It is widest in the extreme north of First Ridge (up to 100 yards broad) and diminishes thence in both directions to vanishing point in Shell Bay West and at the southern end of Studland Bay.

The Dune-Grass zone is double, consisting outwardly of *Psamma arenaria* with a varying mixture of *Agropyron* spp. and *Festuca rubra*, and inwardly of a wider belt where these species are accompanied by a number of others. The more characteristic of these associates are:

<i>Agrostis tenuis</i>	<i>Hypochoeris radicata</i>
<i>Carex arenaria</i>	<i>Jasione montana</i>
<i>Erythraea Centaurium</i>	<i>Leontodon taraxacoides</i> (hirtum)
<i>Hypochoeris glabra</i>	

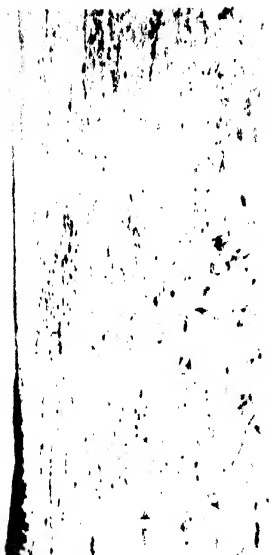
and among the more restricted are:

<i>Aira caryophyllea</i>	<i>Holcus lanatus</i>
<i>A. praecox</i>	<i>Polypodium vulgare</i>
<i>Cerastium vulgatum</i>	<i>Sedum anglicum</i>
<i>Calystegia Soldanella</i>	<i>Senecio Jacobaea</i>
<i>Filago minima</i>	<i>S. sylvaticus</i>
<i>Hieracium umbellatum</i>	

In late summer the yellow Composites are very conspicuous.

(3) *Dune-Heath* (Plates XXIV-XXVI).

This name is given to the whole sequence of vegetation states containing both *Psamma* and ericoids. It begins with an occasional plant of *Erica cinerea* among dominant *Psamma* and ends in a practically closed heath in which *Psamma* merely remains as widely scattered starved plants. Taking into account the extent of this vegetational change, it is not surprising that Dune-Heath is by far the most widespread type of vegetation in the Eastern Sands, covering all but the outer edges of First Ridge, all Second Ridge, and all Inner Ridge and Lone Dunes. Third Ridge has no *Psamma* nor has Southern Heath, so that the time taken for the complete passage from *Psamma* to true heath is here not more than that represented by the difference in age between say First Ridge North and Third Ridge. Since the former has been deposited this century and the latter was first laid down about 1700 it would seem that the successional duration of Dune-Heath on South Haven Peninsula is about 200 years.



Phot. 5. Shore of Studland Bay opposite Pipley Hollows. Line of young *Psamma* with a few strand plants stretches north as the foundation of a new dune ridge.



Phot. 7. Southern Heath and Little Sea. Lone Dunes in right middle distance; Curlew Clump in background.



Phot. 6. Southern Heath and Little Sea. 3-acre and 12-acre Woods and reed swamps in background.



Phot. 8. First Ridge, Lone Dunes in left middle distance.

Photographs 6, 7 and 8 from a panorama from sea beach to south end of Little Sea, taken looking north from the highest part of First Ridge south, and showing the passage of vegetation from pure *Psamma* on the shore edge (8) to bracken heath on the edge of Little Sea (6).

The characteristic species of Dune-Heath are:

<i>Agrostis tenuis</i>	<i>Hypochoeris radicata</i>
<i>Calluna vulgaris</i>	<i>Jasione montana</i>
<i>Carex arenaria</i>	<i>Leontodon taraxacoides</i> (hirtum)
<i>Cuscuta Epithymum</i>	<i>Polypodium vulgare</i>
<i>Erica cinerea</i>	<i>Psamma arenaria</i>
<i>Erythraea Centaurium</i>	<i>Rumex Acetosella</i>
<i>Festuca rubra</i>	<i>Sedum anglicum</i>
<i>Filago minima</i>	<i>Senecio Jacobaea</i>
<i>Hypochoeris glabra</i>	<i>Ulex europaeus</i>

It will be noticed that, excluding the ericoids, all but three of these are species also of the Dune-Grass. As these die out sooner or later in the Dune-Heath development it follows that this leads to a marked diminution of species, and the ultimate heath condition is one of the poorest of all the peninsula communities in number of species.

(4) *Dune-Gorse* (Plate XXVI, 14).

In certain local spots *Ulex europaeus* replaces *Erica cinerea* as the prominent forerunner of more stable vegetation on the dunes, and there results an open association, dominated by this species, which is here called Dune-Gorse. It occurs in two very definite areas, namely between the south edge of South Haven Flats and the north end of Plateau Heath, and as a middle zone in Northern Dunes.

Floristically Dune-Gorse differs from Dune-Heath chiefly in the much greater amount of *Ulex europaeus* and in the significance or, even locally, the complete absence of the ericoid plants, but in addition there occur several species which do not normally occur in the Dune-Heath. Among them may be instanced:

<i>Aira praecox</i>	<i>Lotus corniculatus</i>
<i>Anthoxanthum odoratum</i>	<i>Plantago Coronopus</i>
<i>Erythraea pulchella</i>	<i>Sagina procumbens</i>
<i>Erodium cicutarium</i>	<i>Stellaria graminea</i>
<i>Festuca ovina</i>	<i>Teucrium Scordonia</i>
<i>Geranium molle</i>	<i>Trifolium dubium</i>
<i>Holcus lanatus</i>	<i>Veronica arvensis</i>

It is significant that many of these species are found also in some of the damp sand localities (see below), and from this point of view Dune-Gorse may be regarded as intermediate between Dune-Heath and damp sand vegetation. As the difference between the habitats of these two is most conspicuously one of water content it would seem that the substrate under Dune-Gorse is intermediate as regards this character also.

(5) *Dry Heath* (Plates XXIII-XXV).

This may be defined, at least on the Eastern Sands, as the ericoid vegetation from which *Psamma* has completely died out and in which *Calluna vulgaris* and *Erica cinerea* predominate over *E. Tetralix*. It is found on the main southern part of Third Ridge and on the eastern edges of Southern Heath proper, that is to say on dry surfaces more than 200 years old. The general species are *Calluna vulgaris*, *Erica cinerea*, *E. Tetralix*, *Carex arenaria* and

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Ulex europaeus, and locally associated with these are *Rubus* spp., *Agrostis* spp., *Jasione montana*, *Juncus squarrosus* and *Pteris aquilina*.

Although there is at first sight great similarity between this Dry Heath and the heath of the Western Plateau, the former has not yet reached equilibrium. Not only do species of the Dune-Heath still persist, but longer vegetational establishment will certainly cause humus changes in the substrate which will become reflected in later communities. It is not possible yet to estimate how long such additional changes will take.

Owing to the absence from it of *Psamma* there must be included under the heading of Dry Heath one particularly localised and isolated area. This is the low island in the middle of Little Sea Swamp. Its exact history and age are uncertain, but it is definitely shown on Sheringham's survey of 1849. The increase of fresh water round it and the consequent development of swamp vegetation has resulted in its becoming bounded, and to some extent covered, by small trees of *Salix cinerea*, *Betula* and occasional *Ilex* and *Sorbus aucuparia*. In the centre, however, the remnants of a heath vegetation are still present in the form of some *Calluna*, *Erica cinerea* and moribund *Ulex europaeus* accompanied by *Carex arenaria*, *Teucrium Scorodonia*, *Agrostis tenuis* and one or two other species. The absence of *Psamma* is doubtless due to the presence of trees and to the peculiar water relations of the spot, since according to its apparent age it should bear the same type of vegetation as the Dune-Heath of First and Second Ridges.

(6) *Bracken-Heath* (Plate XXIV, 6).

Although this vegetation is superficially very unlike Dry Heath, its composition differs only in the additional and dominant presence of the one species *Pteris aquilina*, and the developmental difference is thus small. It is found on the Eastern Sands in two places, i.e. on that part of Third Ridge adjoining Plateau Enclosure and on the western side of Southern Heath. It is significant that these two areas are the oldest in the Eastern Sands and are roughly contemporary, representing the primary sand deposits at the two ends of the peninsula. They thus date from 1700 or rather earlier. Age, however, is clearly not the only factor controlling the presence of bracken, or that species should occur all over the Western Plateau. Probably other factors such as burning play a part, although their effects are not yet fully seen on the Eastern Sands.

(7) *Damp Heath*.

This type of vegetation, which is dominated by *Erica Tetralix* and further characterised by the presence of *Drosera rotundifolia*, *D. longifolia*, *Scirpus caespitosus*, *Salix repens* and sparse *Molinia*, is present on Eastern Sands proper only in a few very local spots among the Dune-Heath or Dry Heath where the substrate is particularly damp or as a transitory condition between some of the damp sand localities and Acid Marsh. It is comparatively well developed in the south-western corner of Southern Heath, but this region is

part of the rather debatable junction of the Western Plateau and the Eastern Sands.

(8) *Damp Sand Communities* (Plates XXV, 11, 12, XXVI, 14).

This type of vegetation is common on Eastern Sands and forms what is perhaps their most interesting feature, not only because of its variety but also because of the richness of its flora. This damp sand vegetation is the counterpart, in the damper prairie, of the Dune-Heath condition in the drier and equivalent to it as a successional state. It is, however, much more variable, and the expression of temporary equilibria between dryness and wetness and

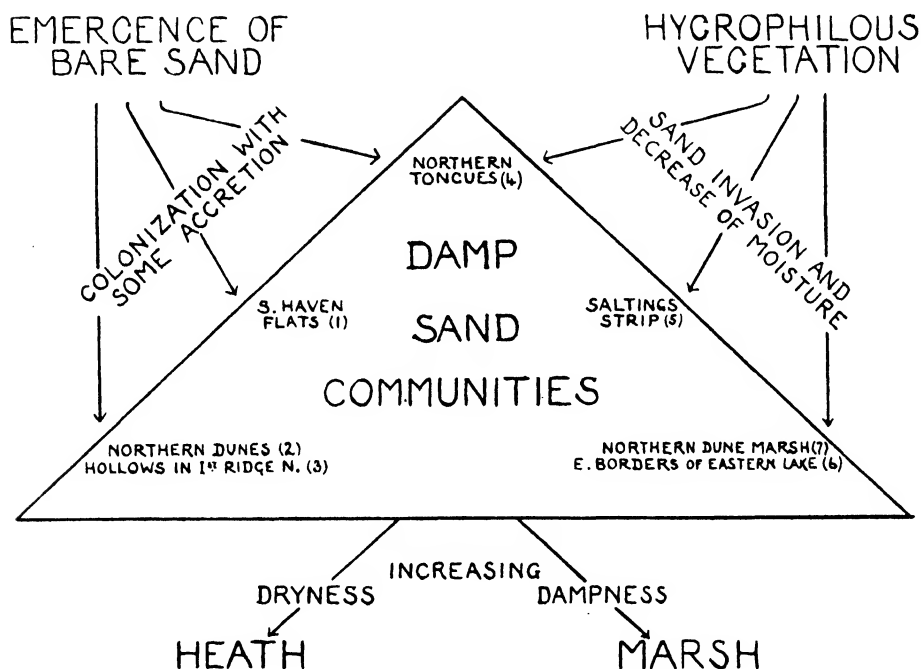


FIG. 2. Diagram to illustrate the development of Damp Sand Communities.

between high and low salinity. It arises in several different ways, primarily by the gradual emergence of sand levels and slacks and their subsequent leaching, but very often from the invasion of existing vegetation of a hygrophilous character by blown sand. These various modes of origin are illustrated in diagrammatic form in Fig. 2.

This diagram includes seven separate and numbered localities, and their general floristic features can best be described by means of the following table in which is given the distribution of the more characteristic species over these localities. No other species have been recorded from more than two of the seven localities.

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	Localities						
	1	2	3	4	5	6	7
<i>Agrostis tenuis</i>	x	x	x	x	x	x	x
<i>Leontodon taraxacoides</i> (hirtum)	x	x	x	x	x	x	x
<i>Juncus articulatus</i> (lampocarpus)	x	x	x	x	x	x	x
<i>Radiola linoides</i>	x	x	x	x	x	x	x
<i>Sagina procumbens</i>	x	x	x	x	x	x	x
<i>Scirpus setaceus</i>	x	x	x	x	x	x	x
<i>Carex arenaria</i>	x	x	x	x	x	x	.
<i>Erythraea Centaurium</i>	x	x	x	x	x	x	.
<i>Plantago Coronopus</i>	x	x	.	x	x	x	x
<i>Aira praecox</i>	x	x	x	x	.	x	.
<i>Anagallis tenella</i>	x	.	x	.	x	x	x
<i>Carex Oederi</i>	x	x	.	x	.	x	x
<i>Filago minima</i>	x	.	x	x	.	x	x
<i>Holcus lanatus</i>	x	x	.	x	x	x	.
<i>Lotus corniculatus</i>	x	x	x	.	x	.	x
<i>Juncus squarrosus</i>	x	.	x	x	x	x	.
<i>Luzula campestris</i>	x	.	x	x	x	x	.
<i>Potentilla Anserina</i>	x	.	.	x	x	x	x
<i>Juncus maritimus</i>	x	.	x	x	x	x	.
<i>Calluna vulgaris</i>	x	.	x	x	x	x	.
<i>Cerastium vulgatum</i>	x	x	.	x	.	.	x
<i>Juncus bufonius</i>	x	x	.	x	.	.	x
<i>J. Gerardi</i>	.	.	.	x	x	x	x
<i>Drosera rotundifolia</i>	.	.	x	x	x	x	.
<i>Erica Tetralix</i>	.	.	x	x	x	x	.
<i>Microcala filiformis</i>	.	.	x	x	x	x	.
<i>Trifolium fragiferum</i>	x	.	.	x	x	x	.
<i>Lotus uliginosus</i>	x	.	x	.	x	x	.
<i>Anagallis arvens</i>	x	.	.	x	.	.	x
<i>Erythraea pulchella</i>	.	.	.	x	x	.	x
<i>Sagina apetala</i>	x	x	.	x	.	.	.
<i>S. subulata</i>	.	.	.	x	.	x	.
<i>Rumex Acetosella</i>	x	x	x
<i>Salix repens</i>	.	.	x	x	.	x	.
<i>Aira caryophyllea</i>	x	.	x	.	.	x	.
<i>Osmunda regalis</i>	.	.	x	.	x	x	.
<i>Ranunculus Flammula</i>	.	.	x	.	x	x	.
<i>Sedum anglicum</i>	x	.	.	x	.	x	.
<i>Potentilla erecta</i>	x	x	x
39	31	16	24	31	26	33	19

South Haven Flats (Plate XXVI, 14). This locality is rather unlike the others in several respects. It is drier: it is by far the oldest, being the original tip of the peninsula deposited about 1700: it has, because of its position and stability, been used as a site by man at intervals throughout its history. By the middle of the eighteenth century it was the departure point of a ferry, and a house had been built on it. This and its successors persisted until this century, the latest having finally disappeared in the last 20 years. There are now sundry wooden buildings on it and the cutting of the new road has divided it into two parts.

Vegetationally also it is distinct, being a continuous short turf which tends to become very desiccated in summer, but in the centre is a considerable slightly depressed area in which such hygrophilous species as *Juncus maritimus* and *Anagallis tenella*, together with dwarfed *Calluna*, are conspicuous. It is the only part of the Eastern Sands where there is any indication of stable grassland such as is a common feature of many English psammoseres.



Phot. 9. View looking north from the second Lone Dune from the south. Part of Lone Dune Marsh in foreground; Inner Ridge and associated dunes in middle distance.



Phot. 10. Eastern Lake and the south part of Saltings Strip from south edge of Eastern Lake; taken in 1933 after the making of the New Cut (right background) and subsequent drainage. Second Ridge in background. *Juncus maritimus* conspicuous on edges of lake.



Phot. 11. Damp sand vegetation in the eastern part of Northern Tongues. Scattered patches of *Juncus maritimus*.



Phot. 12. Damp sand vegetation in a hollow in First Ridge North, just north of Central Gap. Sallow and Salix.

Upwards of 100 species have been recorded from it, a figure which is accounted for partly by the presence of common species like *Alechmilla arvensis*, *Bellis perennis*, *Bromus hordeaceus*, *Crepis capillaris*, *Poa annua* and *Rumex crispus*, and partly by the presence of some halophytic species on its western edge. Among the less common species there may be mentioned:

Carex punctata
Festuca ambigua
F. bromoides
Hypochaeris glabra
Moenchia erecta

Ornithopus perpusillus
Sagina nodosa
Trifolium glomeratum
T. subterraneum
Vicia lathyroides

Hollows in First Ridge North (Pl. XXV). These are small and local areas in some of the deeper minor dune valleys. There are two typical examples about half-way along the ridge and another much better one just north of Central Gap. In this last (see Pl. XXV, 12) there are large willow and birch bushes in the centre surrounded by rushes with smaller species on the outside. The smaller hollows tend to lack the willow and birch. In all there is usually some minor sand invasion from the periphery.

Hollows in Northern Dunes. These are more stable and turfy than those on First Ridge and without the arboreal species. Besides the species given in the table above, only *Festuca ovina* and *Sagina maritima* have been noted.

Northern Dune Marsh. This is an old dune "slack" east of Northern Dunes. It may once have been an arm of Central Marsh, to which it reaches, and may have drained into Shell Bay, but this exit, if it ever existed, is now blocked by the newly formed dunes at its north end. In the centre the vegetation is marsh, but surrounding this, especially towards the north end, is a wide border of damp sand. The species here are, with the exception of *Solanum nigrum*, all in the table above.

Saltings Strip (Centre and South) and Northern Tongues. These two must be considered together because although their vegetation is now somewhat dissimilar they are closely related topographically and historically.

Saltings Strip originated as the main valley between Second and First Ridges. It appeared during last century, and towards the end of that period was mapped as Salt Marsh dominated by *Juncus maritimus*. Since then the final building of First Ridge and the formation of new dunes in Shell Bay have isolated the strip and barred both the entry of salt water from the sea and the exit of fresh water from the growing Little Sea. As a result the *Juncus* marsh has lost much of its character and many of its former species have become replaced by fresh-water species, but meanwhile in addition to this there has been repeated sand encroachment over the floor of the Strip. This is clearly seen in the sections of the upper substrate afforded by the sides of the freshly made New Cut, in which there are layers of organic matter separated by thicker layers of clean sand. In the north the marsh is little altered (see below), but in the centre and south it is much modified. Halophytic species have given place to other hygrophytes, but more especially, owing to the sand

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invasions, to plants characteristic of damp sand. This is the reason why these parts of the Strip are classified here and not under marsh, this procedure giving the truest picture of the vegetation as a whole.

The flora is rich, chiefly because in addition to the species in the table there are many such others as *Epilobium palustre*, *Galium palustre*, *Eleocharis* spp., *Hydrocotyle*, *Iris pseudacorus*, *Lythrum Salicaria*, *Molinia*, *Lycopus* and *Oenanthe Lachenalii*, all of which tend to be more plentiful in the south. *Juncus maritimus* is plentiful throughout, and along the edges, particularly in the south, *Salix cinerea*, *Betula* and *Alnus* occur fairly frequently.

Northern Tongues are to-day a closed branched system of valleys in the dunes of the extreme north-east corner of the peninsula. They have certainly developed their present character since 1900, and they probably originated as a branch of Saltings Strip when the dunes to the east began to form. Whether they were originally *Juncus* marsh which has since become partly dried out by sand encroachment or whether they were dry slacks which have become wetter owing to the overflow from Little Sea is uncertain, but on the whole the first supposition seems more likely. The *Juncus*, for instance, appears to be in a relict condition and persisting against pressure of other species rather than in the state of a fresh coloniser. At all events the vegetation to-day is that typical of dry sandy places, and the hygrophilous species are much less in evidence than in the Strip itself. There are, however, quite a number of other plants in addition which in view of the history of the area are of some interest. These are:

Epilobium palustre
Galium palustre
Glaux maritima
Hieracium Pilosella
Hypochoeris radicata
Jasione montana

Myrica Gale
Ophioglossum vulgatum
Pulicaria dysenterica
Sagina nodosa
Senecio Jacobaea
Trigonella ornithopodioides

East margins of Eastern Lake (Pl. XXVI, 13). Moving south from the Saltings Strip to Eastern Lake the effect of fresh-water influence from Little Sea becomes more marked and the vegetation rapidly more aquatic. Coincidentally the amount of sand encroachment from the east increases. The result is a series of damp sand habitats formed by the overwhelming of the normal lake margin flora by sand invasion. Although treated as one in the diagram on p. 391, this series is not actually continuous but consists of three separate localities. The first may be described as the general eastern edging of the lake proper; the second is the bed of a deep and narrow bight in the extreme south-east corner of the lake; the third is a similar bight a little farther west.

The table on p. 392 shows that the flora of these three is rich and has much in common with that of the Northern Tongues, a point further emphasised by the presence in one or more of the areas of *Galium palustre*, *Glaux*, *Hydrocotyle*, *Jasione*, *Myrica*, *Ophioglossum* and *Trigonella*. Similarly the general



Phot. 14. South Haven Flats looking south, west of the New Road. Small *Juncus maritimus* in foreground; dune-gorse vegetation in middle distance.



Phot. 16. Northern part of Northern Dune Marsh showing invasion by blown sand. *Juncus maritimus* to left; *Psamma* to the right, and buried plants of *Myrica Gale* associated with it.



Phot. 13. Looking across the extreme south-easterly bight of Eastern Lake to the dunes of First Ridge; showing damp sand and vegetation derived from slight sand invasion of marsh.



Phot. 15. South Haven Saltings from north-east corner of Northern Enclosure, showing rapid invasion of blown sand westwards over dominant *Juncus maritimus*.

presence of *Salix cinerea* and *Betula* shows affinity with Saltings Strip south. On the other hand, the vegetation of the lake margins contains the following species rare or absent in the other damp sand habitats of the peninsula, namely, *Eleocharis palustris* and *E. multicaulis*, *Drosera longifolia*, *Centunculus*, *Scirpus filiformis*, *Ornithopus perpusillus*, *Littorella* and *Peplis Portula*. Finally in the southern bight there are present the following aquatic species clearly derived from the adjacent lake: *Hypericum elodes*, *Eriophorum angustifolium*, *Rumex Hydrolapathum*, *Scirpus fluitans* and *S. maritimus*, *Lycopus* and small *Phragmites*.

(9) *Salt Marsh* (Pl. XXIII, 1 and 2).

There are two places in Eastern Sands where the vegetation, being relatively pure *Juncus maritimus*, merits the name of Salt Marsh, namely the northern ends of Saltings Strip and Central Marsh, but there are great differences between them.

The former is that part of Saltings Strip immediately south of the new sand-bar now separating it from the beach of Shell Bay. Here the encroachment of sand and the flooding of Little Sea has been felt least, and the vegetation remains more nearly than elsewhere that of the original salt marsh. *Juncus maritimus* is very abundant and dense and the only plentiful associate is *Potentilla Anserina*. *Juncus Gerardi* is almost the only other halophytic plant. Towards the north end there are few other species, but towards the south there is a gradual passage to the damp sand vegetation of the central part of the Strip, and many of the plants characteristic there begin to appear.

The vegetation at the north end of Central Marsh is much more typical salt marsh because its communication with the shore has not yet been seriously interfered with by the formation of new dunes and there is still tidal influence. This salt-marsh area is unique in Eastern Sands in having a substrate not entirely composed of marine sand. This came about in the following way. When South Haven Point first appeared it was as the northern extremity of the general dune line which formed Second Ridge. Since this extended considerably further north than Third Ridge the exit of the valley between the two ridges was on the western (harbour) side of the point, so that the lowest part of the valley became covered with a layer of alluvial silt from the harbour, and it is largely on this area that the present salt marsh occurs. Then when Central Cut was made fresh water from the Little Sea made its influence felt. Later, when the new road was made, the drainage exit to the harbour was blocked, and this drainage water began to escape by a new exit across the beach into Shell Bay. Most recently the redistribution of sand accretion consequent upon the erosion of Shell Bay has tended to block even this eastern exit, thereby repeating the processes which took place earlier in Saltings Strip.

At present the Salt Marsh consists of two parts—a smaller northern part,

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now almost merged with the Shell Bay shore and suffering rapid sand invasion, and a larger southern portion, as yet comparatively unaltered. In the former the vegetation is scanty, consisting of *Juncus maritimus* and, on the east, of *Spartina Townsendi* with a few other ordinary salt-marsh species.

The southern portion of the marsh itself consists of two parts, the more natural part called South Haven Saltings and the somewhat artificial Northern Enclosure. The latter dates from the earlier nineteenth century and seems never to have been more than the limitation of the normal *Juncus* vegetation by a bank, for the purposes of rough pasture. In both parts the *Juncus* is very abundant and almost pure (some is cut annually), but the associated species change from north to south as the salinity decreases. This is shown in the following table. The south-west corner of the enclosure is now occupied by marsh vegetation that has spread from the south.

	South Haven Saltings	Northern Enclosure		South Haven Saltings	Northern Enclosure
<i>Aster Tripolium</i>	×	.	<i>Festuca rubra</i>	×	×
<i>Carex arenaria</i>	×	.	<i>Juncus maritimus</i>	×	×
<i>C. extensa</i>	×	.	<i>Leontodon taraxacoides</i>	×	×
<i>Glaux maritima</i>	×	.	<i>Oenanthe Lachenalii</i>	×	×
<i>Juncus bufonius</i>	×	.	<i>Potentilla Anserina</i>	×	×
<i>J. Gerardi</i>	×	.	<i>Schoenus nigricans</i>	×	×
<i>Lotus corniculatus</i>	×	.	<i>Sieglingia decumbens</i>	×	×
<i>Plantago Coronopus</i>	×	.	<i>Trifolium repens</i>	×	×
<i>Salicornia</i> sp.	×	.	<i>Carex binervis</i>	.	×
<i>Scirpus maritimus</i>	×	.	<i>Cerastium vulgatum</i>	.	×
<i>Spergularia marginata</i>	×	.	<i>Holcus lanatus</i>	.	×
<i>Suaeda maritima</i>	×	.	<i>Hypochoeris radicata</i>	.	×
<i>Triglochin maritimum</i>	×	.	<i>Lotus uliginosus</i>	.	×
<i>Agrostis alba</i>	×	×	<i>Rosa canina</i>	.	×
<i>Anagallis tenella</i>	×	×	<i>Samolus Valerandi</i>	.	×
<i>Atriplex</i> sp.	×	×	<i>Trifolium fragiferum</i>	.	×
<i>Erythraea Centaurium</i>	×	×			

(10) *Acid Marsh*

This name has been given here to include the vegetation states which serally connect Damp Sand or Damp Heath with Swamp. In respect of these they represent a somewhat generalised condition containing species occurring in all of them. They are fairly widely developed but do not show any very consistent constitution, although two facies are particularly notable. The first of these is practically damp heath in which the smaller monocotyledonous species (*Molinia* and smaller *Junci*) are especially common. The second may be described as a reduced form of swamp lacking some of the larger and more conspicuous plants.

The chief locality of Acid Marsh is in the main part of Central Marsh between Northern Enclosure and the southern swamp, and here the two facies mentioned are particularly well seen, that nearer Damp Heath occurring in the north and that nearer Swamp in the south. Elsewhere Acid Marsh is found in a number of isolated localities of which East Marsh and the surroundings of New Pool are the chief.

The history of the central part of Central Marsh is clear. It originated as the main valley between Third and Second Ridges and thus dates from about 1750. Whether in the early days it bore any vegetation is uncertain. In maps of 1785 and 1849 it is shown as sand but without information as to the plants if any. By 1849, however, Northern Enclosure had been formed and the first effects of the formation of Little Sea were to be seen in a marsh, presumably salt, with *Juncus maritimus*, at the southern end of the valley. Between this and the similar marsh at the north end it would seem likely that there must have been Dune-Grass or Dune-Heath.

The southern marsh died out soon after, apparently chiefly as a result of the making of Central Cut, and in 1886 the site was rough pasture. Soon after this, however, the final damming of Little Sea occurred and Central Cut became inadequate. The general water level rose and the whole Central Marsh valley became flooded, resulting, as Diver says, in the extension of marsh conditions over 1400 yards in the course of 24 years. The bed of the valley is not, however, quite level and there is a marked minor summit level not far south of Northern Enclosure. Here the valley is crossed by a series of low, plant-covered sand-hills with marsh between. From this point south the level gradually falls and the result is, botanically, very interesting as it has led to the development of a marsh graded southward from almost a damp heath state to that of typical swamp and there are thus exhibited in linear series many of the earlier successional stages of swamp.

Actually the vegetation of the marsh, although graded, is not so complicated as might be expected and the whole can be fairly accurately generalised as a *Molinia-Myrica-Erica Tetralix* marsh. These three species, together with *Betula alba*, *Calluna*, *Potentilla erecta*, *Rubus*, *Salix cinerea* and *Ulex europaeus* occur throughout. Commonly associated with them in the north and centre are:

Anthoxanthum odoratum
Cnicus palustris
C. pratensis
Drosera rotundifolia
Erica cinerea
Holcus lanatus
Leontodon hispidum

Lotus uliginosus
Pteris aquilina
Salix repens
Scirpus caespitosus
Sieglingia decumbens
Stellaria graminea

while towards the south most of these give place to such species as:

Bidens cernua
Galium palustre
Hydrocotyle vulgaris
Juncus effusus
J. sylvaticus (acutiflorus)

Lastrea aristata
Lonicera Periclymenum
Lycopus europaeus
Rumex Hydrolapathum

The marsh area next in importance is East Marsh and the sequence of events by which its vegetation has developed is almost equally clear. The substrate was probably originally deposited early last century during the formation of the northern ends of southern ridges, but it was not until after 1900 that the present plant cover began to develop as a result of the flooding caused by the rise of the water in Little Sea. East Marsh may, in fact, be

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called a drowned Dune-Heath. To-day its vegetation is a *Molinia-Myrica-Juncus effusus* community with the following associated species:

<i>Betula alba</i>	<i>Juncus maritimus</i>
<i>Carex Goodenowii</i>	<i>J. squarrosus</i>
<i>Drosera longifolia</i>	<i>J. sylvaticus (acutiflorus)</i>
<i>D. rotundifolia</i>	<i>Lastrea aristata</i>
<i>Eleocharis palustris</i>	<i>Osmunda regalis</i>
<i>Erica Tetralix</i>	<i>Potentilla erecta</i>
<i>Eriophorum angustifolium</i>	<i>Ranunculus Flammula</i>
<i>Hydrocotyle vulgaris</i>	<i>Salix cinerea</i>
<i>Juncus bulbosus</i>	

A very similar vegetation is seen in what remains of Northern Dune Marsh.

Round New Pool in Third Ridge is a wide and wet area showing an intermediate condition between Acid-Marsh and Swamp (see *infra*). The species here are:

<i>Eleocharis palustris</i>	<i>Myrica Gale</i>
<i>Hypericum elodes</i>	<i>Osmunda regalis</i>
<i>Juncus maritimus</i>	<i>Potamogeton polygonifolius</i>
<i>Molinia coerulea</i>	

The remaining marsh habitats are all in the south of the peninsula and are much alike. Surrounding and dividing the largest of the Lone Dunes on Southern Heath is a series of three small marshy patches. They were originally slacks formed when the dunes were piled and have gradually increased in wetness. One is dominated by *Molinia*, another by that species and *Erica Tetralix* and the third by half grown *Osmunda*. Pibley Hollows are somewhat similar local depressions in Southern Heath. They are irregular in size and shape and suggest an artificial origin. Lastly there is the definitely artificial habitat of Pibley Sand Pit, an extensive excavation in Southern Heath made towards the end of last century. It now has a somewhat drier facies than the other places mentioned.

The following species occur in all these minor habitats:

<i>Betula alba (small)</i>	<i>Juncus effusus</i>
<i>Drosera longifolia</i>	<i>Molinia coerulea</i>
<i>D. rotundifolia</i>	<i>Osmunda regalis</i>
<i>Erica Tetralix</i>	<i>Juncus bulbosus</i>
<i>Hydrocotyle vulgaris</i>	

while others of common occurrence are:

<i>Calluna vulgaris</i>	<i>Potentilla erecta</i>
<i>Carex Goodenowii</i>	<i>Salix cinerea</i>
<i>Eleocharis palustris</i>	<i>S. repens</i>
<i>Juncus conglomeratus</i>	

(11) *Acid Bog.*

In a few scattered areas in the older parts of Eastern Sands, where there has long been accumulation of water, typical deep *Sphagnum*-bog is seen. There are actually three such habitats, two of them in the middle of Third Ridge and the other in Southern Heath, and all are of roughly the same age. It must not be supposed however that their development has necessarily followed a continuous course since their inception. The largest is One-acre Pool, a name which indicates the approximate size of the area in 1924. It is

somewhat larger now. This may have developed in the slack between the original shore and the first sand deposits, but its history is obscure and cannot usefully be discussed here. Its present state of maximum water is very recent. It is now a more or less open area of water containing a few species and surrounded by a boggy zone containing numerous others. These are for the most part segregated according to very local conditions. The following species are characteristic of the centre of the pool:

Agrostis alba
Eleocharis palustris
Hypericum elodes
Juncus bulbosus

Menyanthes trifoliata
Potamogeton polygonifolius
Ranunculus Flammula

and the following occur in the surrounding zone:

Anagallis tenella
Drosera rotundifolia
Eleocharis uniglumis
Eriophorum angustifolium
Galium palustre
Hydrocotyle vulgaris

Juncus effusus
J. maritimus
Lonicera Periclymenum
Pinguicula lusitanica
Rubus sp.
Ulex europaeus

Just south of One-acre Pool, and occupying another hollow in the same valley, is New Pool, so called because its aquatic condition seems to be of very recent origin. It is much smaller than One-acre and first appears, in the map of 1924, as marsh. In 1933 the centre of the pool actually dried out, but there remained surrounding it the very wide wet zone described above under marsh. The seven species recorded from the pool itself are, except for *Scirpus fluitans*, also recorded from One-acre.

The remaining Acid Bog is in the series of three similar but even smaller pools in Southern Heath. These Pibley Pools are much alike vegetationally and it is sufficient to say that in all of them occur *Drosera longifolia*, *Eleocharis multicaulis*, *Hypericum elodes*, *Hydrocotyle vulgaris*, *Juncus bulbosus*, and *Molinia coerulea*. The southern pool appears on the map of 1886. The others are shown as marshy patches in 1894.

(12) *Swamp* (Pl. XXVII).

Swamp, that is to say vegetation developed in shallow standing water, dominated by *Phragmites* or the larger species of *Scirpus* and *Juncus*, and including much *Salix cinerea*, *Betula* and *Myrica*, is one of the most widespread vegetational conditions in Eastern Sands and is found wherever the augmentation of Little Sea has shallowly flooded the neighbouring land surfaces, as along the edge of most of Little Sea proper, the south part of Central Marsh, and in Eastern Lake. It is absent from the south-eastern borders of Little Sea where the shore is very abrupt.

True Reed-Swamp dominated by *Phragmites*, almost pure, occurs only in three places, and the great bulk of the Swamp vegetation is mixed, in the sense that it contains all or nearly all the species mentioned above and none is particularly outstanding. The largest reed-swamp is that which fills the southern extremity of the Little Sea. A second but much smaller one is in

the south-eastern corner of the central part of Central Marsh. In addition to these there are scattered patches of reed along the south-west shores of Little Sea. These are but a pale reflection of the first named.

This Little Sea reed-swamp is certainly older than the others, as it is shown as such on the geological field sheets of 1894, a time when the entry of tidal water into Little Sea had barely ceased and it was no doubt the diluting effect of the fresh-water drainage through Piplely Swamp that made so early a development possible. Where the reed-swamp abuts on Piplely Swamp and Piplely Enclosure there are zones of transitional vegetation, but the species recorded actually associated with the *Phragmites* of the reed-swamp proper are:

<i>Agrostis tenuis</i>	<i>Lotus uliginosus</i>
<i>Carex Goodenowii</i>	<i>Lycopus europaeus</i>
<i>Eleocharis palustris</i>	<i>Menyanthes trifoliata</i>
<i>Epilobium palustre</i>	<i>Myriophyllum spicatum</i>
<i>Eriophorum gracile</i>	<i>Potamogeton polygonifolius</i>
<i>Galium palustre</i>	<i>Potentilla palustris</i>
<i>Hydrocotyle vulgaris</i>	<i>Ranunculus Flammula</i>
<i>Hypericum elodes</i>	<i>Salix cinerea</i>
<i>Juncus bulbosus</i>	<i>Scutellaria minor</i>
<i>J. conglomeratus</i>	<i>Typha latifolia</i>
<i>J. sylvaticus (acutiflorus)</i>	<i>Utricularia major</i>

The reed-swamp in Central Marsh is bounded on the east by a bank. It is comparatively isolated and its flora is much less rich than that of the Little Sea swamp. It also shows considerably more relation with the mixed swamp vegetation (below), as is illustrated by the occurrence in it of such plants as *Molinia*, *Myrica*, *Lastrea aristata*, *Rumex Hydrolapathum*, and *Solanum Dulcamara*.

It is appropriate to mention here a very remarkable plant society which at one spot occurs associated with Reed-Swamp. This is the vegetation now seen between the reed-swamp at the eastern end of Spur Bog and the bog itself. It may be actually on the old shore, but since it has clearly arisen as the result of the drowning out of the eastern part of the bog by the growth of Little Sea, it is included here. It is a community, mostly of *Polytrichum* and *Sphagnum*, in which both reach what must be nearly their maximum size. They occur in dense patches capable of bearing the human body, and among them the following species occur. It will be noticed that they are a mixture of bog and swamp plants:

<i>Agrostis</i>	<i>Juncus maritimus</i>
<i>Betula alba</i>	<i>J. sylvaticus (acutiflorus)</i>
<i>Calluna vulgaris</i>	<i>Menyanthes trifoliata</i>
<i>Drosera anglica</i>	<i>Molinia coerulea</i>
<i>D. longifolia</i>	<i>Myrica Gale</i>
<i>D. rotundifolia</i>	<i>Osmunda regalis</i>
<i>Eleocharis multicaulis</i>	<i>Phragmites communis</i>
<i>E. palustris</i>	<i>Potentilla erecta</i>
<i>Eriophorum angustifolium</i>	<i>Rhynchospora alba</i>
<i>Hydrocotyle vulgaris</i>	<i>Salix cinerea</i>
<i>Hypericum elodes</i>	<i>Scirpus Tabernaemontani</i>
<i>Juncus bulbosus</i>	<i>Utricularia major</i>

Mixed Swamp, as described above, is found throughout the remainder of the margins of Little Sea except where, as is rarely the case, there is no bounding vegetation, and it is one of the most conspicuous botanical features



Phot. 17. General view of northern part of Little Sea from south part of Curlew Heath, showing the extensive Little Sea Swamp and Western Arm Marsh. *Agrostis setacea* plentiful in foreground; *Pteris* in middle distance.



Phot. 18. Southern edge of Little Sea Swamp, showing the wide raft of floating *Scirpus fluitans* and *Hypericum clodes*. The butterfly net indicates the height of the *Phragmites*.



Phot. 19. Another aspect of the *Hypericum clodes* rafts in the same region. Taken looking west across Little Sea Enclosure and Spur Heath.

of the peninsula. In most places it takes the very characteristic form of a landward belt of larger species and a waterward belt of rafts of *Hypericum elodes*, locally associated with *Scirpus fluitans*, floating far out into the water (see Pl. XXVII, 18 and 19). These rafts are astonishingly stable, and it is possible and often convenient to walk along them. Its greatest development is in Little Sea Central, where, on the west side, it forms Little Sea Swamp and Western Arm Marsh, and, on the east, a broad belt west of North-South Dyke. It is least and locally absent on both sides of Little Sea Southern I.

Over so wide an area there are naturally many variations in the floristic constitution of this Swamp vegetation, and it must suffice here to give in one classified list all the species that have been recorded from it.

Plentiful and characteristic species.

<i>Betula alba</i>	<i>Myrica Gale</i>
<i>Galium palustre</i>	<i>Phragmites communis</i>
<i>Eleocharis palustris</i>	<i>Potamogeton polygonifolius</i>
<i>Hydrocotyle vulgaris</i>	<i>Ranunculus Flammula</i>
<i>Hypericum elodes</i>	<i>Salix cinerea</i>
<i>Juncus bulbosus</i>	<i>Scirpus fluitans</i>
<i>J. maritimus</i>	<i>S. maritimus</i>
<i>J. sylvaticus (acutiflorus)</i>	<i>S. Tabernaemontani</i>

Common but relatively inconspicuous species.

<i>Agrostis alba</i>	<i>Lotus uliginosus</i>
<i>Bidens cernua</i>	<i>Lycopus europaeus</i>
<i>B. tripartita</i>	<i>Mentha aquatica</i>
<i>Carex Goodenowii</i>	<i>Menyanthes trifoliata</i>
<i>Epilobium palustre</i>	<i>Molinia coerulea</i>
<i>Eriophorum angustifolium</i>	<i>Osmunda regalis</i>
<i>Holcus lanatus</i>	<i>Potentilla palustris</i>
<i>Juncus conglomeratus</i>	<i>Rubus sp.</i>
<i>J. effusus</i>	<i>Rumex glomeratus</i>
<i>J. subnodulosus (obtusiflorus)</i>	<i>Scutellaria minor</i>
<i>Lastrea aristata</i>	<i>Solanum Dulcamara</i>
<i>Lonicera Periclymenum</i>	

More uncommon or local species, often on the edges only.

<i>Anagallis tenella</i>	<i>Oenanthe crocata</i>
<i>Anthoxanthum odoratum</i>	<i>Potentilla erecta</i>
<i>Drosera longifolia</i>	<i>Scirpus parvulus</i>
<i>D. rotundifolia</i>	<i>Stellaria uliginosa</i>
<i>Juncus articulatus (lampocarpus)</i>	<i>Ulex europaeus</i>

Outside Little Sea, Mixed Swamp vegetation is found at the south end of Central Marsh and in Eastern Lake. The former is of special interest on account of its history. In 1849 this area was shown in the same way as Little Sea Swamp and was certainly marsh, presumably saline, but in the next thirty years this marsh died out and in 1886 it is shown as "rough pasture". There is evidence that it was grazed. With the rise of Little Sea it became again waterlogged, so that the 1900 map shows it as marsh once more, but now fresh rather than saline. Since that time the further accumulation of fresh water has brought it to its present condition. It is thus now the result of two successive oscillations between dryness and wetness and at present shows a maximum in the latter state. It is one of the best developed of the mixed

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swamps, with a denseness and depth that make it almost impenetrable. This is particularly due to the "chevaux de frise" effect of the large *Myrica* bushes which abound in it and to the rank tussocky nature of the rest of the vegetation. Its area is fairly definitely circumscribed and lies for the most part south of East-West Dyke, but it extends far north as a narrow border to Central Cut, which was made about 1868 to control the water in Little Sea.

The chief species of this swamp are:

Eriophorum angustifolium
Juncus conglomeratus
J. effusus
J. maritimus
J. sylvaticus (acutiflorus)

Myrica Gale
Osmunda regalis
Rumex Hydrolapathum
Scirpus Tabernaemontani

Associated with these, upwards of twenty other species have been recorded. Of these all but five, i.e. *Iris Pseudacorus*, *Schoenus nigricans*, *Triglochin palustre*, *Typha latifolia* and *Veronica Anagallis-aquatica*, occur also in the Little Sea swamps. In addition the (locally) rare species *Alisma Plantago-aquatica*, *Apium nodiflorum* and *Lemna minor* have been noted in the Central Cut.

Eastern Lake (Pl. XXV, 10), the third of the Mixed Swamp habitats, was formed between 1894 and 1900. At first it communicated with the shore through a gap in the dunes, but this has now been closed for some years. The lake is divisible vegetationally into three parts—the north and south borders, the western end towards North-South Dyke, and the centre of the lake proper. In the first two of these the vegetation is very much like that already listed for Little Sea swamps except that the species are generally more conspicuously zoned and include such additions as *Erica Tetralix*, *Iris Pseudacorus*, *Rumex Hydrolapathum*, *Alnus rotundifolia*, *Schoenus nigricans* and *Salix aurita*.

The centre of the lake in 1932 contained a rather open vegetation of the larger rushes and sedges, with much open water about a foot deep between them more or less filled with smaller aquatic plants. *Scirpus Tabernaemontani* was specially conspicuous in the middle, giving a green facies in contrast to the browner tint of the margins. The bottom of the lake was covered with a submerged species of *Hypnum*.

In 1933, after the lake was drained by the making of New Cut, the *Hypnum* remained as a dried layer of an inch or two on the bottom. The *Scirpus* was smaller and grazed by the cattle which wander over the peninsula. During the winter of 1933–4 a further cut was made connecting the lake with Little Sea across North-South Dyke so that the lake became once more filled with water as it had been in 1932. In view of these vicissitudes and their possible effect on the vegetation it is worth quoting in full the list of species recorded from the central part of the lake in 1932. They are:

Agrostis alba
Eleocharis palustris
Hydrocotyle vulgaris
Hypericum elodes
Hypnum sp.
Iris Pseudacorus
Juncus maritimus

Lycopus europaeus
Ranunculus Flammula
Rumex Hydrolapathum
Scirpus fluitans
S. maritimus
S. Tabernaemontani
Utricularia major

(13) *Sallow-Birch Thicket.*

The actual areas over which *Salix cinerea*-*Betula* thicket exclusively occurs are small, but these two species are constituents of many of the communities already described and especially in the swamps and marshes. Their rapid increase in the last thirty years is one of the major ecological developments of the peninsula. It has led also to a considerable change in the general appearance of Eastern Sands, since they are, with comparatively rare exceptions, the only arboreal species in this region.

The general distribution of these plants as associated species has already been given, but in one part of the peninsula they tend to become dominant. This is along the edges of Central Marsh and here, locally, there are well-grown Sallow-Birch thickets. One of the best is in the extreme north-west not far from Northern Enclosure, but there are others further south. The soil in them is brownish black with a great deal of humus and there is good undergrowth. Exactly what are the conditions favouring the development of these thickets is not clear, but it may be noted that they most often occur where Dune Heath or Heath meets Marsh or Swamp, and it may be that they follow a line of particular soil water values. Both the tree species seem able to tolerate wide variation of salinity. As is indicated in the diagram on p. 386, Sallow-Birch Thicket is the most highly developed type of vegetation on Eastern Sands. As is to be expected from their successional and spatial relationships, the smaller species found in these thickets are in part heath species, in part marsh species, and to a small extent woodland species. Among the latter *Listera ovata* and *Poa pratensis* may be mentioned as elsewhere rare or absent. The distribution of Sallow-Birch thickets on Eastern Sands is indicated by the deciduous tree symbols on the detailed topographical map.

(14) *Open aquatic.*

Only in Little Sea is there any submerged aquatic vegetation unassociated with subaerial species. This is not rich but contains one or two particularly rare and noteworthy species. The list is:

<i>Callitriche autumnalis</i>	Scattered.
<i>C. intermedia</i>	Scattered.
<i>Elatine hexandra</i>	Recently recorded. A very inconspicuous species plentiful in the centre and parts of the south.
<i>Isoetes echinospora</i>	First recorded about 10 years ago. Abundant over most of the central part and extends into the south. In places the plants are almost continuous.
<i>Juncus bulbosus</i>	General but belonging more properly to the marginal vegetation.
<i>Myriophyllum spicatum</i>	Here and there on the east side.
<i>Potamogeton polygonifolius</i>	Especially in the north and south.
<i>Scirpus nanus</i>	More properly a marginal species long known from the south-east side. As there have been radical changes in its habitat since it was discovered, the plant is probably now diminishing.
<i>Utricularia major</i>	Another local species here not uncommon in the shallower parts.

By 1886 tidal influences were no longer felt in Little Sea except on rare occasions, and these species have presumably nearly all become established since then.

(15) *Other communities* (Pl. XXVI, 15, 16).

Even behind the newer dune deposits the substrate in many parts of Eastern Sands is by no means stable, and several times in the preceding pages reference has been made to the effect produced on various vegetation states by renewed or continued sand accretion. For a long period after the appearance of more consolidated conditions such as dune heath the vegetation is still an open one, and there is ample opportunity for the removal or augmentation of the dry sand between the individual plants. As a result sand redistribution of one kind or another is a common feature in this part of the peninsula. Gravity and the effect of rain may denude the more elevated deposits, or "blow-outs" may be developed by wind action, as is well seen on Lone Dunes. But these are of minor importance compared with the much greater changes which are constantly taking place as a result of new dune formation on a large scale. This is happening to-day on two sides of the peninsula, namely Shell Bay and Studland Bay, but there is an essential difference in detail between the two. In Studland Bay the deposition of the new dunes is taking place on a virgin base, that is to say on the inner line of the shore, which, except perhaps for a few strand plants, has no plant life. Quite otherwise in Shell Bay. Here the formation of new dunes is accompanied by marked erosion of the bay itself so that the new dune line is laid down on top of pre-existing vegetation into which the erosion has eaten. In addition to these processes there appears to be also in the northern part of Studland Bay a slow and gradual drift of sand westwards.

Resulting from all these factors it is not surprising to find many small areas in Eastern Sands, where, owing to sand encroachment, the vegetation, instead of being typical of one of the conditions already described, is anomalous in the sense that it contains species characteristic of more than one of them. One of the most marked of these sand invasions, that at the north-east corner of South Haven Saltings, has already been mentioned under the heading of Salt Marsh, but there are several others. A particularly striking one is at the north end of Northern Dune Marsh (see Pl. XXVI, 16) where Acid Marsh is being smothered by freshly blown sand. Here many of the marsh plants have disappeared, but *Myrica* and one or two others persist and are to be seen almost covered by the sand. Other good examples occur at the northern end of Saltings Strip, where sand has been deposited in quantity across the old *Juncus maritimus* vegetation.

It was stated above (p. 379) that Eastern Lake formerly drained towards Studland Bay shore through a gap in the dunes which is now closed by sand deposition. Evidence of this is still to be seen just west of the present Central Gap where there is now a flat sandy area bearing not only dune species but also such Swamp relics as *Juncus maritimus*, *J. Gerardi* and *Scirpus maritimus*.

Lastly, much blown sand has been piled at the south end of Pipleys Sand

Pit on top of the old marsh vegetation. As the sand encroaches, first *Erica Tetralix* then *Calluna* disappear, and there are finally left the four species *Agrostis tenuis*, *Carex arenaria*, *Jasione* and *Sedum anglicum*.

ACKNOWLEDGMENTS.

My grateful thanks are due to many who have given me help with this work in one way or another and particularly to Mr L. Beeching Hall, not only for his assistance in the identification of species but also for his services as guide during preliminary visits to the Peninsula; to Mr Hamilton-Fletcher for much important local information; and to Capt. C. Diver, whose remarkable knowledge of the area has been most freely put at my disposal and who was largely responsible for the initiation of the work. I am also much indebted to Prof. Tansley for his helpful criticism and advice.

OBSERVATIONS ON THE ECOLOGY OF THE CENTRAL DESERT OF ICELAND

BY F. W. ANDERSON AND P. FALK.

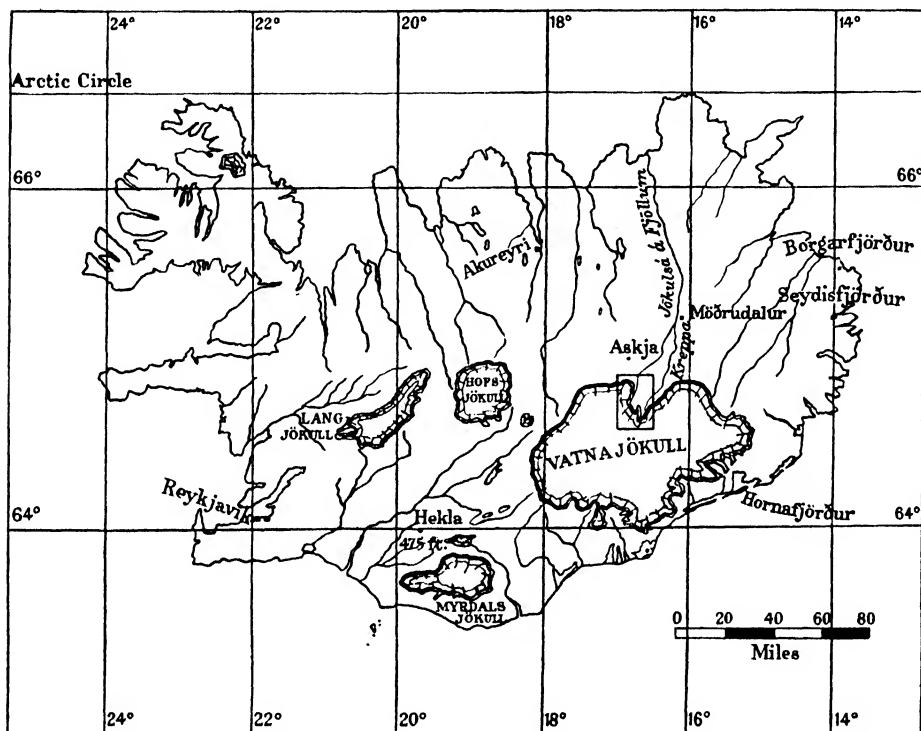
(With Plates XXVIII–XXX, and two Maps and two Diagrams in the Text.)

THE central plateau of Iceland consists of a desert of lava, gravel and blown sand, bounded on its southern edge by an irregular line of small ice-caps. The whole of this area, which is unfit for human habitation, occupies about two-thirds of the island, i.e. about 70,000 sq. km. The largest of the ice-caps, Vatnajökull (8000 sq. km.), is the southern boundary of the least known part of the desert, and it is with part of this area that the present paper is concerned. On the north side of Vatnajökull is a mountain of volcanic origin, Kverkfjöll (lat. $64^{\circ} 45' \text{ N.}$, long. $16^{\circ} 37' \text{ W.}$), and from it Kverkfjallarani, a series of volcanic ridges, runs north into the desert for about 35 km. From each side of Kverkfjöll rivers run north from the ice-cap, and these, combined with the desolate nature of the country, have made the area so inaccessible that its plant and animal life were almost unknown and the eastern scarp of Kverkfjöll was not discovered until the Cambridge Expedition of 1932 (1). This expedition reached Kverkfjöll on July 14th by crossing Vatnajökull from the south coast; it established its base camp there and a smaller party then travelled as far into the desert as the oasis, Hvannalindir (see map on p. 408). Owing to the shortage of time, only eight working days, and the difficulties of transport, nothing more than a preliminary survey could be made.

The desert is composed almost entirely of basalt which has weathered very rapidly, leaving great scree slopes with loose spaces of weathered lava between them. In places also the ground is strewn with large boulders of lava, often of fantastic shapes (Pl. XXVIII, phot. 2). The proximity of volcanic action to the ice-cap which is probably rapidly receding, renders the area peculiarly attractive for an ecological survey, though Max Trautz (2), who travelled to Kverkfjöll in 1912 and has summarised the investigations of earlier explorers, has written of it: "Kein Tropfen Wasser..., keine Spur von Leben barg sich hier." The only attempted botanical survey of the area is due to Thoroddson (3), who travelled along the north of Vatnajökull in August 1884, but was unable to collect plants from Hvannalindir, owing to a snowstorm.

No exact meteorological information is available, but the mean annual temperature of Möðrudalur, 40 miles north of Kverkfjöll, is -0.4° C. , and owing to the height above sea-level and the presence of the ice-cap, the annual

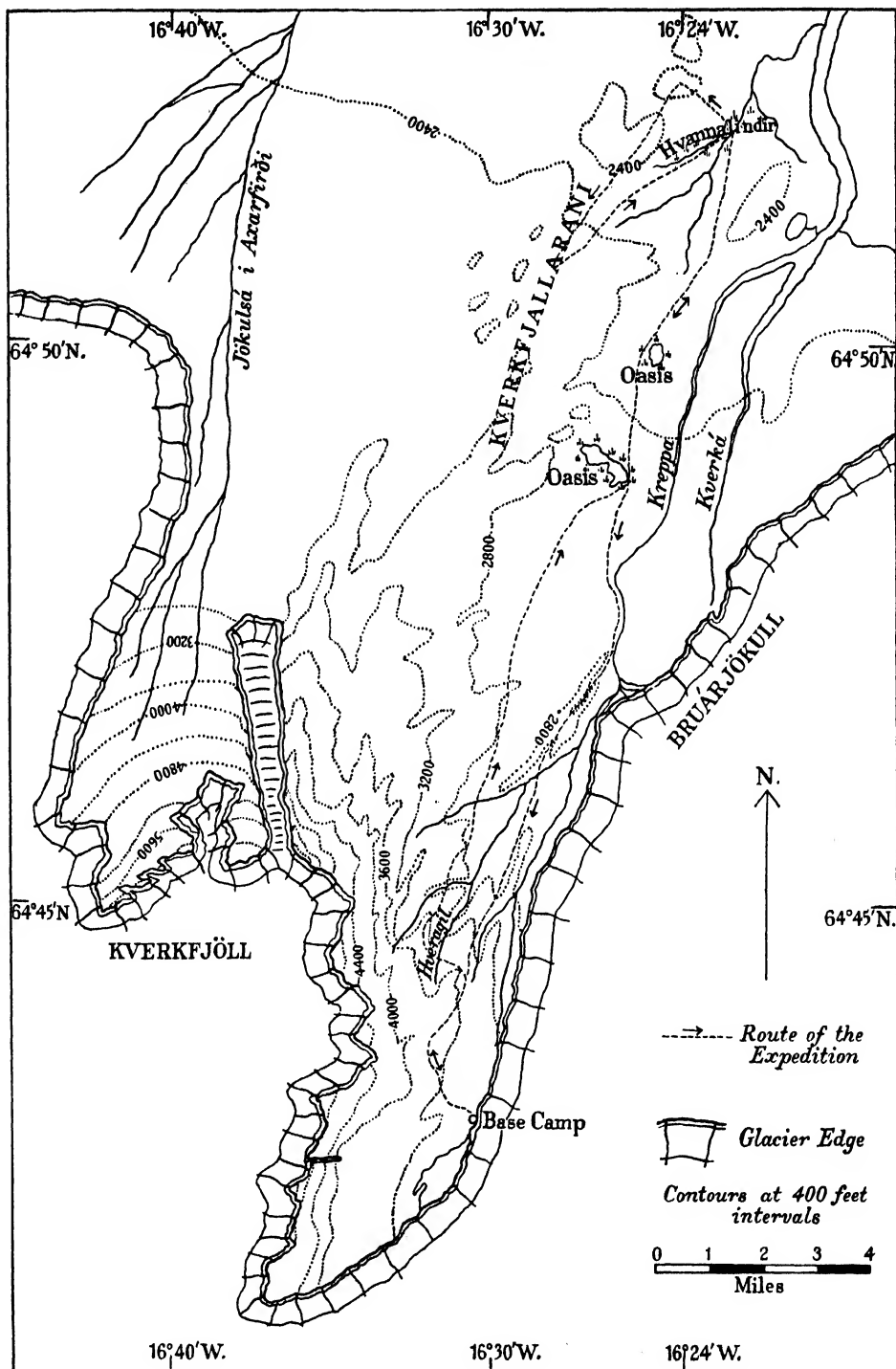
mean of this area is estimated by Thoroddsen to be -2°C . At the end of July 1932, the mean day temperature was 6°C ., and the mean night temperature 3°C . The total annual precipitation at Borgarfjörður on the east coast, the nearest recording station, is 46 in., and that of the desert is probably greater. Of this precipitation the greatest amount is probably snow, and this may fall at any time of the year. Though there are no records, it is likely, by comparison with other parts of Iceland, that the whole area is snow-covered from September till May. In spite of this precipitation the soil is so



MAP 1. Sketch-map of Iceland. Area shown in larger map is enclosed in a square.

porous that the surface, when not covered by snow, is always dry, and within half an hour of a heavy rainstorm, a sandstorm may rage in the same place.

The general appearance of the whole area is not unlike that of a sub-tropical desert, with high dune-like hills and sandy flats between them. Except for the few oases, however, the desert is entirely black, and only in the south Vatnajökull shines white on either side of Kverkfjöll, and a large glacier runs through the cleft in the mountain (Pl. XXVIII, phot. 4). There are four chief vegetational habitats, viz. scree slopes and valleys, oases, hill tops and hot springs.



MAP 2. Map to illustrate the route of the Expedition. From the surveys by Trautz, and Lewis and Beckett.

I. SCREE SLOPES AND VALLEYS.

The screes and valleys bear almost no vegetation. In the south of the area, very occasional plants of *Cerastium alpinum*, *Arabis petraea*, and *Armeria maritima* occur, with *Silene maritima* and *Elymus arenarius* farther north. The first two species are of prostrate habit and have the power of rapid stem elongation after covering by sand.

Elymus arenarius was never found growing very far from water, and its occurrence was probably regulated by the depth of the water table below the soil surface. It gave rise to dune formation very similar to that found on the Norfolk coast of England. Stages could be traced in the gradual binding of the soil by the expanding root and rhizome system until a dune 2 ft. high was formed. At this stage no further colonisation by other species occurred, probably owing to the drought caused by the raising of the soil surface so far above the water table. Wind erosion seemed invariably to follow, and thus colonisation by *Elymus arenarius* never led to the establishment of permanent vegetation.

Lichens were almost entirely absent in the desert, even from the rocks of lava. A species of *Usnea* was found very occasionally. The moss *Racomitrium canescens* was also occasionally found. The surprising absence of lichens in a northern desert is probably also due to the rapid weathering of the rocks and the constant movement of their surface.

Owing to the almost complete lack of vegetation on the scree slopes and in the valleys, there is no ground fauna of any description in this zone. The Base Camp, however, was visited every day by large numbers of Diptera, coming from the oases. Two species only were represented, the yellow dung-fly, *Scatophaga stercoraria* L., which was first met with several miles out on the ice-cap and continued to infest the camp; and the bristle-fly, *Calliphora uralensis* Villen. Other visitants to the Base Camp were two caddis-flies (*Limnophilus griseus* L.) and an occasional Chironomid, the latter, unfortunately, not surviving the rigorous transport conditions well enough to be identifiable. On the screes, two individuals only were seen in an area of approximately 25 sq. miles, both harvestmen, and of the same species, *Mitopus morio* Fabr.

Two species of birds only were observed in the desert away from the oases. Two Snow Buntings (*Plectrophenax nivalis insulae*) were seen near Kverkfjöll, and a solitary specimen of this bird was also observed by Trautz there (2). It can only be regarded as a visitor from the oases. A dead Faroe Snipe (*Capella gallinago faeroensis*) was also found at Kverkfjöll.

II. THE OASES (Pl. XXIX, photos. 5-8).

Though the lava is extremely porous, springs and rivers occur in the desert, and this must be due to the underground formation of the lava flows. Round the springs there is vegetation and two oases were examined. The first of these, previously unknown, consisted of a lake with springs at one end, but

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no exit, so that the water must drain out through the lava at the other end. The second, Hvannalindir, had already been visited eleven times, but its vegetation and animal life had not been examined before. In it the vegetation surrounded the banks of several streams and occupied the lowest part of the area included between the bends of the streams. The vegetation in both oases was very similar, so that they may be treated together. It was always in zones round the water, in correlation with the height of the soil surface above the water table.

At the edge of the oases and wherever the soil level rises slightly within them the ground is very sparsely covered with the ordinary scree plants (*Arabis petraea*, *Cerastium alpinum*, *Armeria maritima*, *Silene maritima*) and also:

<i>Silene acaulis</i> L.	<i>Saxifraga nivalis</i> L.
<i>Saxifraga decipiens</i> var. <i>Groenlandica</i> L.	<i>Erigeron alpinum</i> L.
<i>S. oppositifolia</i> L.	<i>Oxyria digyna</i> L.

These plants never extend more than a few yards towards the loose, bare desert or lava rocks ((Pl. XXVIII, phot. 2) called "hraun" by the Icelanders). This zone (zone A in Diagrams 1 and 2) was also very sharply defined on its inward side. The only representatives of a ground fauna were Arachnida: the Harvestman, *Mitopus morio* Fabr., wandering freely over the sand, and the spider *Erigone arctica* White, found by turning over stones. (At the first oasis *Atheta atramentaria* Gyll. was found in this zone, and under the stones red mites.) In the air *Scatophaga squalida* Mg. and Chironomidae were common, and the black-fly, *Simulium vittatum* Zett., fairly common.

Within this area was a distinctive community (zone C in Diagrams 1 and 2) dominated by the two willows *Salix lanata* L. and *S. phylicifolia* L. These formed quite a close covering over the ground, the mosses growing round the roots of the flowering plants. In spite of this, however, there were frequent places where erosion by the wind had exposed the roots of the willows and the mosses were absent. These "blow-outs" (Pl. XXX, phot. 11) were often colonised by *Carex nardina* and *Equisetum arvense* and more rarely by *Carex capillaris* and *C. microglochin*, plants otherwise confined to the damper parts of the oases. The floral composition of this community is given below, plants absent from the first oasis being marked with an asterisk:

<i>Salix lanata</i> L.	l.d.	* <i>Trisetum spicatum</i> L.	r.
<i>S. phylicifolia</i> L.	l.d.	* <i>Festuca arenaria</i> L.	r.
<i>S. herbacea</i> L.	f.	* <i>Poa trivialis</i> L.	r.
<i>Poa alpina</i> var. <i>vivipara</i> L.	f.	<i>Carex incurva</i> Lightf.	r.
<i>Calamagrostis neglecta</i> Fr.	f.	<i>C. capillaris</i> L.	r.
<i>Polygonum viviparum</i> L.	f.	<i>C. nardina</i> Fr.	r.
* <i>Euphrasia latifolia</i> Pursh.	f.	<i>C. microglochin</i> Wahlenb.	r.
<i>Deschampsia alpina</i> R. et Sch.	o.	* <i>Empetrum hermaphroditum</i> Hagerup	
<i>Equisetum arvense</i> L.	o.	(one plant only)	

The following mosses also occurred:

<i>Webera cruda</i> Schwaeg.	<i>Swartzia montana</i> Lindb.
<i>Aulacomnium palustre</i> Schwaeg.	<i>Conostomium boreale</i> Swartz.
<i>Hypnum polygamum</i> Schp.	<i>Philonotis fontana</i> var. <i>tomentella</i> Dixon
<i>H. exannulatum</i> Guemb.	<i>Rhacomitrium canescens</i> Brid.
<i>H. falcatum</i> Brid. var. <i>gracilescens</i>	<i>Leptobryum pyriforme</i> Wild.
<i>Swartzia inclinata</i> Ehrh.	<i>Encalypta rhabdocarpa</i> Schwaeg.



Phot. 2. Desert covered with crags of basalt (hraun).



Phot. 3. The cone at Hvannalindir rising from the desert.



Phot. 1. The desert looking north-east; Vatnajökull on the right. In the centre steam is rising from the hot springs.



Phot. 4. The desert, looking south towards Kverkfjöll in the distance. (Caption text is partially cut off in the original image.)

Of the fauna of this zone much the commonest form was the Geodephagan, *Nebria gyllenhali* Schönh., this beetle being especially abundant where the soil was highest and driest. On the inner edge of the zone where the soil was wetter *Atheta atramentaria* Gyll. was commonly found, usually under moss. The dung-flies, *Scatophaga stercoraria* L., *S. squalida* Mg., *S. villipes* Zett. and *Fucomyia frigida* F. were present in large numbers, chiefly on goose dung

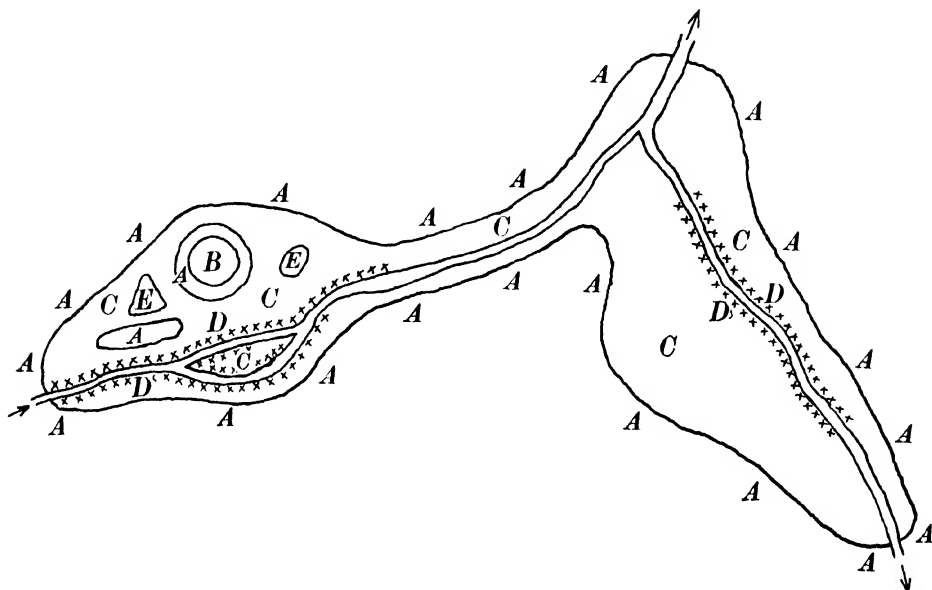


DIAGRAM 1. Sketch-map (not to scale) of Hvannalindir to show the distribution of plant and animal communities. A, bare scree with *Arabis petraea*, etc. and *Elymus* dunes. B, volcanic cone with hilltop community. C, willow community. D x x x, riverside community with *Archangelica* and *Epilobium latifolium*. E, Swamp with *Eriophorum Scheuchzeri*.

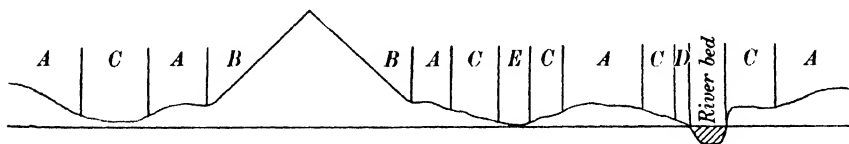


DIAGRAM 2. Ideal cross section to show all the possible types of community.

and apparently depositing their eggs on it. *Calliphora uralensis* was also present and very common. Two crane-flies were captured in this zone, *Rhaphidolabis exclusa* Walk., fairly abundant, and *Ormosia holtedahli* Alex., rare. Of the Hymenoptera occasional ichneumons were found, *Pimpla* sp. and *Hemiteles* sp., and a few larvae of the saw-fly (subfamily Nemertinae). At the first smaller oasis the fauna of this zone differed slightly. Of the ground fauna, *Erigone arctica* White was also the dominant form. One species of the large carnivorous beetle, *Creophilus maxillosus* L., was collected, the only one seen north of the

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ice-cap. Other Coleoptera were, *Nebria gyllenhali* Schönh. and *Atheta grammicola* Grav. The volant forms were represented by *Scatophaga stercoraria* L., dominant, *Tipula rufina* Mg., *Crymodes excilis* Lef., and several small indeterminate flies belonging to various Acalyptiate families.

On the banks of the streams, the vegetation differed from the willow community described above. The mosses became denser, and at Hvannalindir, where the banks of the stream were steep, the riverside community (zone D of Diagrams 1 and 2) had the following composition (Pl. XXIX, phot. 6):

* <i>Archangelica officinalis</i> Hoffm.	l.d.	<i>Poa alpina</i> var. <i>vivipara</i> L.	o.
* <i>Epilobium latifolium</i> L.	l.d.	<i>Calamagrostis neglecta</i> Fr.	o.
<i>Salix lanata</i> L.	a.	<i>Deschampsia alpina</i> Roem. et Schultz	o.
<i>S. phlycticifolia</i> L.	a.	<i>Juncus balticus</i> L.	o.
<i>Polygonum viviparum</i> L.	a.	<i>Equisetum arvense</i> L.	o.
<i>Salix herbacea</i> L.	f.	* <i>Sagina procumbens</i> L.	r.
<i>Carex incurva</i> Lightf.	f.	<i>Galium pumilum</i> L.	r.
<i>Epilobium alsinifolium</i> Vill.	o.	* <i>Taraxacum officinale</i> Weber	r.
<i>Cerastium alpinum</i> L.	o.		

In addition to the mosses that occurred in the willow community, the liverwort, *Marchantia polymorpha**, was very frequent just above the water edge. There were also numerous fungi, chiefly Agarics and Discomycetes.

The usual volant forms were present: Lepidoptera—*Rhyacia conflua* Tr., *Crymodes excilis* Lef., and *Cnephasia osseana* Scop., usually found on the petioles of *Archangelica*; Trichoptera—*Limnophilus griseus* L., *Apatania arctica* Boh.; Diptera—*Simulium vittatum* Zett., *Scatophaga stercoraria* L., *Tipula rufina* Mg., with *Meioneta* sp. and Thrips, the last only found in the petioles of *Archangelica*.

At the first oasis, where the banks were not steep and the water was not flowing, the willow community persisted to the water edge, and the riverside community, described above for Hvannalindir, was entirely absent. Its place was taken, where the water level had dropped very recently, by a few plants of *Catabrosa aquatica* and *Ranunculus hyperboreus*, which must normally have been submerged, and *Ranunculus paucistamineus* var. *eradicatus* floating on the surface. Owing to the steep banks of the stream at Hvannalindir, these species were not found there. The only animals found here on the mud surface between the scattered plants were specimens of the water beetle, *Agabus bipustulatus* L. From the analysis of a stomach content the floating *Ranunculus paucistamineus* var. *eradicatus* was recognised as forming the main food of a pair of Whooper Swans (*Cygnus cygnus islandicus*) which were swimming on the water of the oasis.

In both oases in damp hollows which had once been connected with the main supply of water, but had become cut off by a fall in the water level, a third community existed (zone E of Diagrams 1 and 2; Pl. XXIX, phot. 8). The hollows had practically no standing water, except immediately after rain; the drainage was entirely by underground seepage. The dominant plant was *Eriophorum Scheuchzeri*, with abundant *Calamagrostis neglecta* and *Carex*

* Species not found at the first oasis.



Phot. 5. The river bank at Hvannalindir, Kverkfjallaráni in the background. The willows in the distance cease abruptly as the soil rises above the water level. The banks are too high for the riverside community.



Phot. 7. Springs at Hvannalindir; *Elymus* dunes in the distance. Vegetation is confined to the banks of the streams and the low-lying area on the right. In the foreground are mainly willows and some *Archangelica* in the lower distance.



Phot. 6. The riverside community at Hvannalindir, containing *Archangelica officinalis*. On the far side of the stream and in the foreground is the willow community, with *Salix phylicifolia*, *S. lanata*, *Calamagrostis neglecta*, etc.



Phot. 8. A depression with community dominated by *Eriophorum Scheuchzeri* in the middle distance.

incurva and occasional *Epilobium alsinifolium*. The mosses, too, showed a very considerable change from the willow community or the riverside community. At Hvannalindir the following mosses also occurred:

Aulacomnium palustre Schwaeg.
Hypnum adreneum Hedw.
Amblystegium filicinum De Not.
Catascopium nigrum Brid.
Philonotis fontana var. *tomentella* Dixon

Meesia trichoides var. *alpina* Boul.
Leptobryum pyriforme Wild.
Polytrichum alpinum L.
Brachythecium rivulare B. et S.
Funaria hygrometrica Sibth.

The community was inhabited by a large number of Chironomidae, and, rather surprisingly, the Harvestman (*Mitopus morio* Fabr.), with the caddis-fly, *Limnophilus griseus* L., as the commonest form, the larvae being particularly abundant. *Simulium vittatum* Zett. and *Diamesia* sp. were also very common, with a few crane-flies, *Rhaphidolabis exclusa* Walk., and an occasional Braconid, *Aspilota nervosa* Hal. Several caterpillars of the moth *Crymodes excilis* Lef. were found, although the adult was not seen in this zone.

The pH of the soil water was measured by a B.D.H. capillator set, and the pH of this *Eriophorum* swamp was found to be 6.5. The water in the lake at the first oasis and in the stream at Hvannalindir was 6.8, and that of the soil of the willow community did not differ appreciably from this. These results are inconclusive, though they indicate the possibility of the effects of humus formation here.

At both oases a number of birds were observed, and the observations on these have already been published (5), so that the results need only be summarised here. At the first oasis (oasis A of Roberts), twenty-eight pairs of Snow Bunting (*Plectrophenax nivalis insulae*) were seen; these were confined to the broken rocky ground (hraun) at the edge of the oasis. No stomach contents were examined, but at Hvannalindir the Snow Buntings were watched catching caddis-flies, apparently their main diet. On the water, at the same oasis, the following duck were observed: two male Harlequin Duck (*Histrionicus histrionicus*), which had probably come up from the Kreppa; and thirteen (nine adult) Long-tailed Duck (*Clangula hyemalis*). Of the latter species, three pairs were breeding, and the young had just hatched (July 17th). In addition to these duck, there were twenty-three Red-necked Phalarope (*Phalaropus lobatus*) on the water.

At a smaller oasis north of this (oasis B of Roberts), included with the first oasis in the other observations, three Snow Buntings, eight Red-necked Phalarope, two Grey Phalarope (*Phalaropus fulicarius*), one Purple Sandpiper (*Erolia maritima maritima*), and a pair of Whooper Swans (*Cygnus cygnus islandicus*) were seen. An examination of the stomach contents of the last species revealed only *Ranunculus paucistamineus* var. *eradicatus* leaves (30 per cent.), *Eriophorum Scheuchzeri* seeds (10 per cent.) and sand and pebbles (60 per cent.). At Hvannalindir, where there was no still water, the duck were absent, and only the following birds were seen: seventeen pairs of Snow Bunting, twelve Red-necked Phalarope, two Purple Sandpiper, five Iceland Ptarmigan

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(*Lagopus mutus islandorum*), two Arctic Skua (*Stercorarius parasiticus*) and one Greater Black-back Gull (*Larus maritimus*). The gull flew up from the north and returned after flying round for a few minutes. The only bird found breeding at Hvannalindir was the Iceland Ptarmigan; there was a single nest in a clump of *Elymus arenarius*, and the young had just hatched out (July 18th). From the examination of the stomach contents of a single specimen, this species was entirely phytophagous without any obvious prejudices; its stomach was found to contain *Salix lanata*, *S. phylicifolia*, *S. herbacea* and *Equisetum arvense* leaves, and also the seeds of *Polygonum viviparum*. At all the oases, goose dung was found, and their call was heard once at Hvannalindir, but no bird was ever actually seen.

In addition to the birds, two other vertebrate animals were recorded. Visits of the Arctic Fox (*Alopex lagopus*) were inferred from its dung, though the animal was never seen, and a few Iceland Char (*Salvelinus alpinus*) were found in a stream near the first oasis. This was remarkable as the stream disappeared within a quarter of a mile of its source.

III. THE HILLTOPS.

On the summits of hills the soil movement must be less than on scree slopes or in valleys, since there cannot be the continual fall of lava particles to which any lower place is subject, and the hilltops were found to support a flora differing considerably from that of the screes or of the oases. Three hilltops were examined in detail: the first, a dome near the northern edge of the glacier (Pl. XXX, phot. 12), the second, a volcanic cone at the centre of Hvannalindir (Pl. XXVIII, phot. 3), and the third a considerable area at the top of Kverkfjallarani, a line of hills about 2 miles west of Hvannalindir, 500 ft. above the general level of the desert.

The dome near the edge of the glacier had a firm surface near its top, and supported a flora confined to the crevices in the lava. In Pl. XXX, phot. 12 the limit of this flora corresponds exactly with the rough outline of the unweathered lava at the top of the dome. The scree below this, which has a smooth outline, supported only the sparse flora characteristic of the desert. This hilltop flora had the following composition:

Cerastium alpinum L.

Silene acaulis L.

Saxifraga oppositifolia L.

S. decipiens var. *Groenlandica* L.

Saxifraga nivalis L.

Oxyria digyna L.

Salix herbacea L.

Poa alpina var. *vivipara* L.

Only one moss was present, *Racomitrium canescens*, and one lichen, *Usnea* sp. A similar flora was found on any place protected from falling lava, and with this flora a characteristic fauna was probably connected, though only two observations were made. Two individuals of a dark form of *Rhyacia confluens* Tr. were collected from small isolated plants, a mile apart, of *Thymus serpyllum*, and occasional specimens of the small Bell Moth (*Cnephasia osseana* Scop.) were found resting on the hilltops.



Phot. 9. Springs at Hvannalindir at the origin of a small stream which soon disappears again beneath the surface. The vegetation is confined to the low lying area on the left.



Phot. 10. Hot springs at the bottom of the gorge at Hveragil. The vegetation can be seen as shining patches on each side of the stream. A little snow is seen high up on the left.



Phot. 11. A "blow out" in the willow community at Staðardalur on the south coast of Iceland, resembling those at Hvannalindir. Note secondary colonisation in the centre of the blow out by *Carex capillaris* and *C. microglochin*.



Phot. 12. Dome near the northern edge of Vatnajökull; hilltop flora occurs only on the rugged upper part, not on the smooth, loose scree below. On the moraine is the base camp. In the foreground is a glacier covered by blown sand.

The cone at the centre of Hvannalindir (Pl. XXVIII, phot. 3) was only 60 ft. high and was probably snow-covered for the same period as the rest of the oasis, but its flora (zone B of Diagrams 1 and 2) was quite unlike that of the willow community surrounding it. The plants occurred in crevices and no difference in frequency was observed on the different sides of the cone.

Cerastium alpinum L.
Silene maritima With.
S. acaulis L.
Arabis petraea L.
Saxifraga oppositifolia L.
S. decipiens var. *groenlandica* L.

Dryas octopetala L.
Thymus serpyllum L.
Salix herbacea L.
Deschampsia alpina L.
Poa alpina var. *vivipara* L.

Racomitrium canescens and *Usnea* sp. also occurred. The fauna, in addition to the forms usually found on the hilltops in the desert, was enriched by migrants from the surrounding oasis. *Rhyacia confluenta* Tr., in each case captured while feeding on the flowers of *Thymus serpyllum*; *Calliphora uralensis* Villen., very common; the dung-flies, *Scatophaga stercoraria* L., *S. squalida* Mg., *Fucomyia frigida* F.; and *Diamesa* sp. usually found on the flowers of *Cerastium alpinum*; all forms which might be found with the usual hilltop flora of the desert, with, as migrants, the beetle *Nebria gyllenhali* Schönh., found under stones, and a species of the family Poduridae (Aptera), always found in the carpels of *Dryas octopetala*. There were only five of these plants in this zone and each contained Poduridae. A conspicuous absentee was the small Brachyelytran, *Atheta atramentaria* Gyll., which was very common elsewhere in the oasis, especially on the wetter ground.

Thirdly, on the top of Kverkfjallarani, a flora similar to that on the cone at Hvannalindir was found, but it differed from it in certain details. The following species occurred:

Cerastium alpinum L.
Silene maritima With.
S. acaulis L.
Arenaria norvegica Gunn
Alsine rubella Wahl.
Arabis petraea L.
A. alpinum L.
Draba rupestris R.Br.
Saxifraga oppositifolia L.
S. nivalis L.
Galium pumilum L.
Saxifraga decipiens var. *Groenlandica* L.

Veronica alpina L.
V. fruticans Jacq.
Armeria maritima Willd.
Taraxacum officinale Weber
Gnaphalium supinum L.
Erigeron alpinus L.
Oxyria digyna L.
Polygonum viviparum L.
Salix herbacea L.
Luzula spicata DC.
Deschampsia alpina L.
Poa alpina var. *vivipara* L.

In places this flora covered the surface of the hilltop and there it consisted of grasses, willows and *Polygonum viviparum*, but more often it merely filled crevices in the lava. In all cases it occurred only in places which were free from the rain of weathered particles of lava. The whole area is about 500 ft. above the general level of the desert and its average temperature is undoubtedly lower. The snow cover is probably of the same duration as that of Hvannalindir, but by comparison with the other two hilltops it seems likely that this flora owes its existence almost entirely to the relatively stable soil surface which it possesses.

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Veronica fruticans, *V. alpina* and *Gnaphalium supinum* all occupy very limited areas, each only a few yards in extent. This was also typical of *Dryas octopetala* and *Thymus serpyllum* at Hvannalindir.

IV. HOT SPRINGS (Pls. XXVIII, 1 and XXX, 10).

In one deep gorge to which the name Hveragil was later given, a series of hot springs was found (Pl. XXX, phot. 10). These occurred about 20 ft. above the river at the bottom of the gorge, and the water from them ran down into the cold water of the river. In the area moistened by the spring water was a particularly luxuriant belt of vegetation not more than 12 ft. across. The hot water flowed first over a rock, which it covered in a continuous sheet, and then over the loose scree, where it was depositing CaCO_3 , which cemented together the loose fragments, thus providing a stable area, the first essential for colonisation of a scree slope.

In the centre, where the water was bubbling up at a temperature of 62° C., there was a mass of alga¹. This grew between temperatures of 54 and 48° C., and in the water with it was a large number of Cypridae. An appreciable amount of the silt beneath was also composed of the empty carapaces of these animals. Next to the hot water of the spring was a zone of warm, wet mud, from 2 to 18 in. wide, covered by *Marchantia polymorpha*, growing far more profusely than on the river bank at Hvannalindir. Surprisingly, the most abundant animal was the Harvestman, *Mitopus morio* Fabr., which with *Hilaira frigida* Thor. and *Nebria gyllenhali* Schönh., made up the whole of the macroscopic fauna of the mud.

Outside this mud zone were three concentric zones each dominated by a different moss. The innermost was dominated by *Brachythecium rivulare*, with which grew *Poa alpina* var. *vivipara* and *Cerastium alpinum*. The fauna was dominated by Spring-tails (Poduridae), with numerous *Erigone arctica* White, *Erigone tirolensis* Koch (rare) and *Atheta atramentaria* Gyll. The grass was festooned with the webs of *Erigone*, but the spider was more often seen at either margin than actually in the grass. The two outer moss zones were considerably drier than this inner zone. The middle zone was dominated by *Philonotis fontana* var. *tomentella* growing with the same flowering plants and *Sagina procumbens*. The outer zone contained the moss *Aulacomnium palustre* together with the flowering plants mentioned above, and in addition *Salix phylicifolia*, *Saxifraga nivalis*, *Epilobium alsinifolium* and a little *Salix herbacea*. The fauna of these two outer moss zones comprised only *Erigone arctica* White, *E. tirolensis* Koch, *Hilaira frigida* Thor., mites and *Borborus* sp. This luxuriant belt of vegetation passes into the characteristic scree flora which rapidly becomes sparser and disappears entirely within 3 yards of the *Aulacomnium* zone. A few animals strayed as much as 9 yards from the

¹ A green alga which unfortunately was destroyed on the sea passage home and has therefore not been identified.

vegetation; these included *Crymodes excilis* Lef., *Calliphora uralensis* Villen., Chironomidae, a few red mites and *Hilaira frigida* Thor. Everywhere in the neighbourhood of the hot springs, and especially gathering over the water itself, were large numbers of Borboridae, Cordyluridae, Chironomidae and Simuliidae depositing their eggs in the decaying algae and in the water.

As the water from the springs must cool in passing from the central algal zone to the outside of the *Aulacomnium* zone, there is a temperature gradient, which appears more likely to be responsible for the zonation of the vegetation than any other factor such as soil movement; the actual quantity of water, however, cannot be excluded from exerting a certain influence, though since each zone was approximately circular, the zonation corresponds more accurately with the temperature gradient than with the water gradient. In this connection it is important that the outer moss zones occurred on the lower side of the belt, where the water was running away, though there they extended only a very small distance. The main factor responsible for establishing colonisation seems to be the deposit of CaCO_3 which stabilises the soil surface. Though there were no species there which were not found at Hvannalindir, the vegetation looked more luxuriant in this small colony than elsewhere in the desert, and this was probably due to the combined influence of a regular water supply and a permanently high temperature.

The seasonal changes in such a colony raise an interesting problem. It was observed that whereas *Cerastium alpinum* and *Poa alpina* were flowering as usual (July), *Saxifraga nivalis*, which was flowering or had flowered elsewhere in the desert, here showed no sign of having flowered or being about to flower. The rosette, which was far larger than usual, bore no scape. It is unknown whether this gorge is snow-covered in the region of the hot springs in winter. A fall of snow of 2 in. in July was found to leave the area of the springs quite free from snow.

V. CONCLUSION AND SUMMARY.

In the four different types of vegetation described, the influence of three different factors can be traced; water supply, soil movement and temperature. The first two factors together are responsible for the absence of vegetation generally in the desert. The height of the soil surface above the water table appears to determine the existence of vegetation zones round the oases. Where the height of the soil surface is not more than about 18 in. above the water level, the riverside community or the swamp dominated by *Eriophorum* can exist. At heights from 18 in. to 3 ft. the willow community exists, and above that only the *Elymus* dunes occur, probably because *Elymus* can survive here by the depth of its root system. Water supply may also be partly responsible for the zonation of mosses at the hot springs.

Movement of the surface soil is responsible for the limitation of such species as *Saxifraga oppositifolia*, *Thymus serpyllum*, etc., to the hilltops. It is only

overcome in three types of places: first in those which are not subject to being covered by falling lava particles; secondly, in places where the plants themselves bind the soil surface together, while their roots can reach down to the water level; and lastly in the hot springs, where the surface is bound together by the CaCO_3 deposit. The effect of wind erosion can be seen especially well in the "blow-outs" in the willow community at Hvannalindir and in the abortive *Elymus* dunes.

The effect of temperature can only be seen at the hot springs, and the way in which it works there has already been discussed. Other places where the effect of temperature might be traced, such as slopes with an abnormally long or deep snow cover (4), were not found.

Owing to the fact that the desert is at present in such an early stage of colonisation, it is possible to reconstruct approximately the way in which the flora and fauna have arrived at their present state of development. Two types of colonisation are found, according to the two different ways in which the moving soil problem is overcome. The first type on the hilltops is still in its earliest stage, and this may account for the limited areas of distribution of such plants as *Veronica fruticans*. Where the vegetation occurs, the fauna immediately follows. The more isolated hilltops with only a few plants supported only visiting Lepidoptera, an occasional *Mitopus*, and such residents as thrips and mites. Where this community is near an oasis and sufficiently large to provide a certain minimum of food for visiting birds, the fauna is enriched by such consequent attendants as the Borboridae, Cordyluridae, Chironomidae, Simuliidae, which may become plentiful enough to support a few *Erigone*.

In the oases colonisation by plants has proceeded to a further degree. The zonation from the water table upwards appears to be static at present, though the appearance of one well-developed plant of *Empetrum hermaphroditum* in the willow community at Hvannalindir suggests that colonisation may be progressing slightly in the direction of the birch climax described by Hansen (4), *Empetrum* being an intermediate stage in the establishment of birch wood (*Betula odorata*) from willow scrub. Such colonisation, however, must be extremely slow, since Hvannalindir was first discovered by Pjetur Pjetursson in 1830 (7) and was then described as good grazing for horses.

The order of colonisation of the oases by animals is a matter of uncertainty, but it seems fairly clear that the first arrivals would be the volant forms in which both adult and larvae are phytophagous, e.g. Lepidoptera, Trichoptera, Tipulidae, followed by *Erigone* which is able to travel long distances attached to an aerial thread, and by the carnivorous Coleoptera, and later by forms dependent on birds for transport, such as *Mitopus*, or on fish, such as *Agabus*. Finally, the parasitic and saprophagous forms such as the Ichneumonidae, Tachinidae, Chironomidae, Borboridae and Cordyluridae, would take their place in the community. The Arctic Fox (*Alopex lagopus*) is the climax of this

community, and though this animal and the birds are only visitors, they are regular visitors and are an essential link in the food chain.

VI. SUMMARY OF SPECIES DETERMINED.

(Where only orders and not species have been determined, the number of species present has been taken as one; the totals given are therefore always the minimum in each case.)

ANIMALS (48 spp.).

Mammalia (1 sp.):

Alopex lagopus (Arctic Fox).

Aves (12 spp.):

Plectrophenax nivalis insulae Salomonsen (Snow Bunting)
Goose sp.
Cygnus c. islandicus Brehm (Iceland Whooper-Swan)
Histrionicus h. histrionicus L. (Harlequin Duck)
Clangula hyemalis L. (Long-tailed Duck)
Phalaropus fulicarius jourdaini Iredale (Grey Phalarope)
P. lobatus L. (Red-necked Phalarope)
Capella gallinago faeroensis C. L. Brehm (Faroe Snipe)
Erolia m. maritima Brünn (Purple Sandpiper)
Larus marinus L. (Greater Black-back Gull)
Stercorarius parasiticus L. (Arctic Skua)
Lagopus mutus islandorum Faber (Iceland Ptarmigan)

Pisces (1 sp.):

Salvelinus alpinus (Iceland Char).

Insecta (26 spp.):

TRICHOPTERA (2 spp.):

Limnophilus griseus L. *Apatania arctica* Boh.

COLEOPTERA (5 spp.):

Nebria gyllenhali Schönh. *Atheta graminicola* Grav.
Agabus bipustulatus L. *Creophilus maxillosus* L.
Atheta atramentaria Gyll.

LEPIDOPTERA (3 spp.):

Crymodes excilis Lef. *Cnephasia osseana* Scop.
Rhyacia conflua Tr.

DIPTERA (12 spp.):

Tipulidae:

Ormosia Holtedahli Alex. *Tipula rufina* Mg.
Raphidolabis exclusa Walk.

Simuliidae:

Simulium vittatum Zett.

Chironomidae:

Diamesa sp.

Cordyluridae:

Scatophaga stercoraria L. *Scatophaga villipes* Zett.
S. squalida Mg.

Coelopidae:

Fucomyia frigida Fabr.

Borboridae:

Borborus sp.; also various acalyptrate forms

Tachinidae:

Calliphora uralensis Villen.

HYMENOPTERA (3 spp.):

Ichneumonidae:

Pimpla sp.

Hemiteles sp.

Tenthredinidae:

Larva of a sawfly, subfamily Nematinae.

Braconidae:

Aspilota nervosa Hal.¹

¹ Not recorded in Lindroth's list of insects (6).

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Arachnida (4 spp.):

Erigone arctica White
E. tirolensis Koch

Hilaira frigida Thor.
Meionata sp.

PHALANGIDEA (1 sp.):

Mitopus morio Fabr.

COLLEMBOLA:

Poduridae spp.

ACARINA:

Species not ascertained.

Crustacea:

Cypridae, species not ascertained.

PLANTS (73 spp.).

Angiosperms (48 spp.):

Ranunculus paucistamineus var. eradicatus L.
R. hyperboreus Rottb.
Silene maritima With.
S. acaulis L.
Cerastium alpinum L.
Alsine rubella Wahl. Whbg.
Arenaria norvegica Gunn
Sagina procumbens L.
Arabis petraea L.
A. alpinum L.
Draba rupestris R.Br.
Dryas octopetala L.
Saxifraga oppositifolia L.
S. nivalis L.
S. decipiens var. Groenlandica L.
Epilobium latifolium L.
E. alsinifolium Vill.
Archangelica officinalis Hoffm.
Galium pumilum Sl.
Gnaphalium supinum L.
Erigeron alpinum L.
Taraxacum officinale Web.
Empetrum hermaphroditum Hagerup
Euphrasia latifolia Pursh.

Veronica fruticans Jacq.
V. alpina L.
Thymus serpyllum L.
Armeria maritima Willd.
Oxyria digyna L.
Polygonum viviparum L.
Salix lanata L.
S. phylicifolia L.
S. herbacea L.
Juncus balticus Willd.
Luzula spicata DC.
Eriophorum Scheuchzeri Hoppe
Carex incurva Lightf.
C. microglochin Whbg.
C. nardina Fr.
C. capillaris L.
Poa alpina var. vivipara L.
P. trivialis L.
Trisetum spicatum L.
Calamagrostis neglecta Beauv.
Deschampsia alpina R. et Sch.
Festuca arenaria Osb.
Catabrosa aquatica Beauv.
Elymus arenarius L.

Pteridophyta (1 sp.):

Equisetales:

Equisetum arvense

Bryophyta:

Musci (19 spp.):

R. canescens Brid.
Webera cruda Schwaeg.
Aulacomnium palustre Schwaeg.
Hypnum polygamum Schp.
H. exannulatum Gruemb.
H. falcatum var. gracilescens Schp.
H. adreneum Hedw.
Swartzia inclinata Ehrh.
S. montana Lindb.
Conostomium boreale Swartz

Philonotis fontana var. tomentella Dixon
Leptobryum pyriforme Wild.
Encalyptra rhabdocarpa Schwaeg.
Amblystegium filicinum De Not.
Catascopium nigrum Brid.
Meesia trichoides var. alpina Boul.
Polytrichum alpinum De Not.
Brachythecium rivulare B. et S.
Funaria hygrometrica Sibth.

Hepaticae (1 sp.):

Marchantia polymorpha

Fungi (2 spp.):

Discomycetes, species not ascertained.

Agaricaceae, species not ascertained.

Lichens (1 sp.):

Usnea sp.

Algae (1 sp.):

Chlorophyceae, species not ascertained.

Total number of species mentioned (animal and plant), 121.

Specimens of most of the above plants and animals were brought back for identification. These were distributed as follows:

- Flowering plants: T. G. Tutin, Cambridge.
- Cruciferae: Dr J. Lid, Oslo.
- Mosses: W. R. Sherrin, British Museum.
- Coleoptera and Lepidoptera: K. G. Blair (British Museum).
- Coleoptera: C. H. Lindroth, Göteborg, Sweden.
- Ichneumonidae: J. F. Perkins, British Museum.
- Braconidae: G. E. Nixon, British Museum.
- Tenthredinidae: R. B. Benson, British Museum.
- Trichoptera: M. E. Mosely, British Museum.
- Diptera: F. W. Edwards and J. E. Collin, British Museum.
- Arachnida: W. R. Sheriffs, Southampton.
- Pisces: J. Berry, Southampton.

To all of these we are extremely grateful for the trouble that they have taken, and especially to Mr K. G. Blair of the British Museum, who in addition to his part in the identification was so good as to distribute our insect material for identification among his colleagues; special thanks are also due to Dr H. Godwin for his kind help in the preparation of this paper and to Mr B. B. Roberts, who supplied all the material in connection with birds given above, and who was also responsible for collecting the insects from the oases.

Specimens of the insects mentioned in this paper are in the possession of F. W. Anderson; the flowering plants, with a few exceptions which it was considered unnecessary to collect, are in the Herbarium of the Botany School, Cambridge; the mosses are in the possession of P. Falk.

Finally, it is a great pleasure to acknowledge the financial help supplied to the expedition by the Royal Society, the Royal Geographical Society, the Wort's Fund, King's College, Emmanuel College and Gonville and Caius College, Cambridge.

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THE VEGETATION OF NAMANVE SWAMP, UGANDA

BY W. J. EGGELING, B.Sc. (FOR.), EDIN.

Assistant Conservator of Forests, Uganda.

(With Plates XXXI–XXXIV, one folding Figure and two Figures in the Text.)

INTRODUCTORY.

NAMANVE SWAMP is situated in Mengo District of Buganda Province in the Uganda Protectorate, between longitude $32^{\circ} 40'$ and $32^{\circ} 43'$ East of Greenwich and latitude $0^{\circ} 17'$ and $0^{\circ} 21'$ North. It opens upon the head of Murchison Bay to the east of Port Bell and is typical of the many similar Papyrus swamps fringing the northern shores of Lake Victoria.

Mainly owing to the proximity of the railway, Namanve was selected in 1928 by the Uganda Forest Department as a suitable area for afforestation with Eucalyptus with a view to the production of fuel. A working plan was accordingly drawn up on the basis of an eight-year rotation, and eight compartments were laid out, one to be planted each year for the period of the rotation.

This reclamation programme has now (1933) been under way for four years, and four compartments have been planted according to plan. The method adopted has been that of mound planting following drainage, as described below.

A main drainage channel 6 ft. wide and 3–4 ft. deep was first cut through the centre of the swamp from its upper end to half-way to open water, a distance of about $2\frac{1}{2}$ miles. Work on Compartment No. 1 then began. Side drains 3×3 ft. were cut along the edges of the compartment and led into the main channel, whilst the vegetation over the area was then slashed down, left for a few days to dry and burnt. Following the burn the compartment was lined out with stakes 10 ft. apart, and at each stake a mound of swamp peat about $2\frac{1}{2}$ ft. high was erected. On these mounds the young Eucalyptus seedlings were planted. This procedure has been followed year by year. At first trouble was taken to see that only finely divided peat was used for making the mounds. All roots, sticks and particles of solid matter were excluded. This was soon found to be a mistake, as during heavy rain the mounds were quickly washed away, and roots are not now removed.

In the first compartment to be planted mixed Eucalyptus plants were used. Results here have not been nearly so successful as in subsequent areas planted with *Eucalyptus robusta* only.

At first when the main drain reached only half-way down the swamp drying was very slow. In 1932, however, the drain was continued to the lake,



Phot. 1. Swamp immediately following slashing and burning. The next stages in reclamation are mounding and planting.



Phot. 2. Drained Papyrus swamp with young Eucalyptus.



Phot. 3. Freshly cut drain in virgin Papyrus swamp. *Cyperus papyrus*, *Miscanthidium violaceum* and *Ficus umbellatus* distinguishable on left.



Phot. 4. Ditch vegetation — *Pistia stratiotes* (water lettuce) and *Ricciocarpus natans*.

and by the end of the year it was possible to say that "in spite of fears in the early stages that the swamp was really too wet ever to be converted into forest, rapid drying continues and two-year-old *Eucalyptus robusta* reaching up to 18 ft. in height are perfectly healthy, and appear to be embarking on a stage of faster growth" (4).

This statement has been amply borne out by the growth shown in 1933, when the best trees were 35 ft. high and the average over 25 ft., three years after planting (Pl. XXXIV, phot. 9).

Object of the paper. It is most desirable that, as the *Eucalyptus* trees grow older, and the swamp dries, records should be kept showing the various stages in the evolution of a plantation flora from a swamp flora, and, subsequently, the changes resulting from clear felling and the growth of coppice. It is hoped that this paper may serve as a useful basis for such a study.

TOPOGRAPHY, SOIL AND CLIMATE.

Namanve lies some 3730 ft. above mean sea-level and is surrounded by low, forest-clad ridges rising some 200 ft. higher. Two rivers, the Nabubaza and Bumbubumbu, drain into Namanve at its northern end, while a third stream enters through Kolo Forest to the east. The swamp is to all intents level, there being a fall of only 8 ft. throughout its length.

Water-level. The level of the water in the swamp varies considerably, depending mainly on the level of Lake Victoria. The lake-level is liable to many fluctuations (1). The most important of these are: (a) periodic variations of 10 in. from month to month, by which the lake is at its highest in May and June, and at its lowest in October and November, and (b) still greater annual variations of nearly 4 ft. from year to year. The yearly fluctuations have been correlated with sunspot numbers, years of lake-level maxima coinciding very nearly with years of sunspot maxima, and years of lake-level minima with years of sunspot minima. The period elapsing between a high-level maximum and a low-level minimum is normally 5-6 years.

This 4 ft. rise and fall is obviously a limiting factor in swamp reclamation work, since, although swamp areas 2-3 miles from the lake might conceivably be planted successfully in years of low lake-level, yet, when the water rose again, they would be hopelessly waterlogged.

In comparison with the above fluctuations precipitation over the Namanve watershed is much less important, and affects only the upper and drier portions of the swamp. A long dry spell automatically lowers the water-level, while prolonged or heavy rain causes a corresponding rise.

Following the cutting of the centre drain, flooding due to local precipitation has been greatly reduced, and is of much shorter duration than previously. Eighteen months after the drain had been put through to the lake the water-level in the top 2 miles of swamp was consistently 15 in. lower than before.

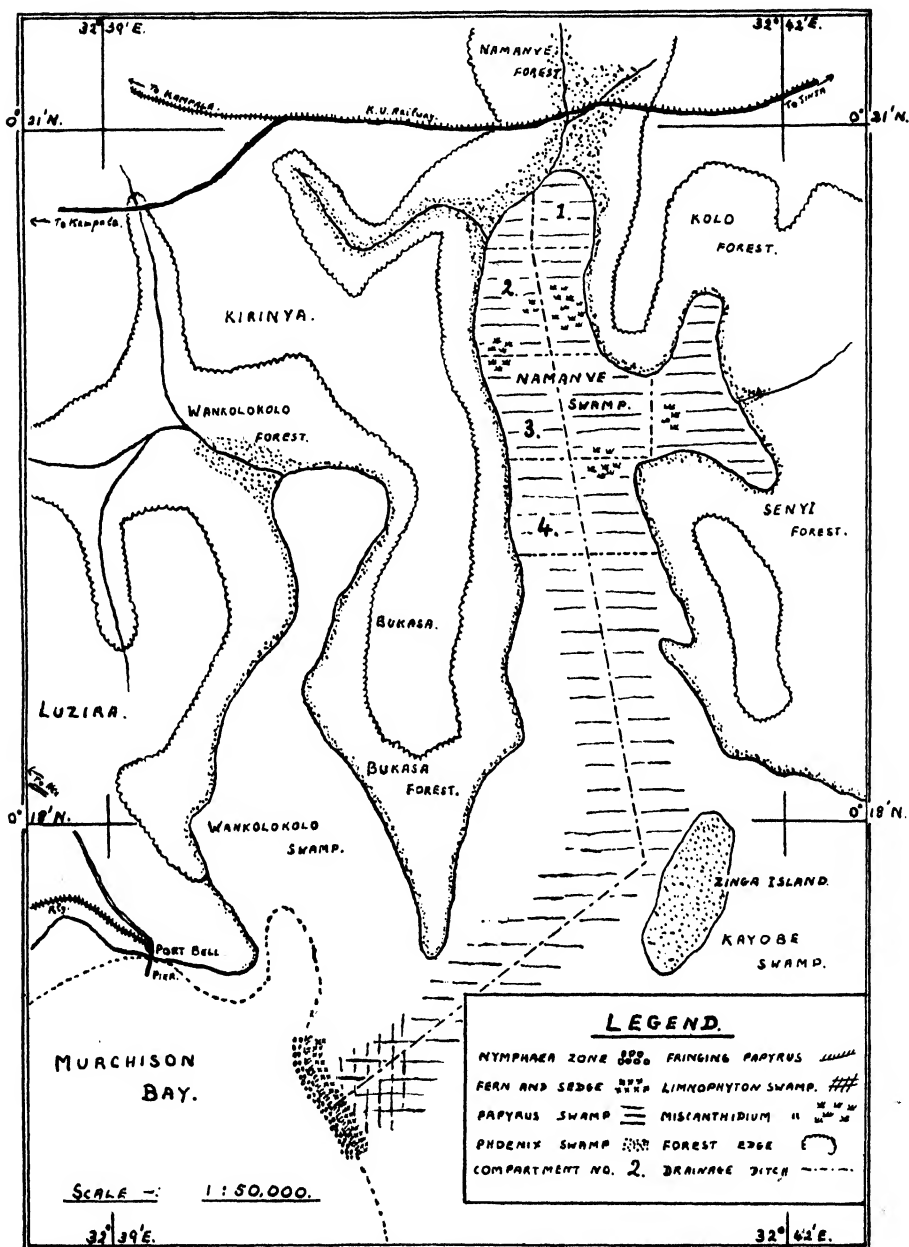


FIG. 1. Sketch-map of Namanve Swamp.

Soil. Except in *Nymphaea* areas the vegetation of Namanve grows upon a layer of decomposing plant remains or swamp peat. In the Kayobe area (see map), this peaty layer is floating, and ranges from 3 in. to 4 or 5 ft. in thickness. In the Namanve area proper the beds appear to rest on the underlying clay, and here the depth of the peat varies from 6 to 7 ft. below the *Miscanthidium* community to at least 8-9 ft. below the papyrus.

Climate. The climate is tropical, relieved by elevation and the proximity of Lake Victoria. There are two wet and two dry seasons. The long rains generally begin in March and may extend into July; the short rains occur normally between September and November. The annual rainfall is somewhat variable but is in the vicinity of 50 in. per annum. January and February are generally the hottest months, May, June and July the coolest.

Fauna. Few mammals reside in the swamp. The most abundant are the water-antelope or sitatunga (*Limnotragus Spekei*), and the clawed otter (*Lutra maculicollis*). Buffalo, leopard, several of the smaller cats, and, at some seasons, monkeys, visit the area for feeding purposes.

Except in near-lake areas birds too are scarce. Lily-trotters (*Actophilornis*), reedhens (*Porphyryla*), black crakes (*Limnocorax flavirostra*), and moorhens (*Gallinula chloropus brachytera*), are typical residents, whilst coucals, weavers, and warblers have also been recorded as nesting. Egrets, herons and a number of Passerines visit the swamp to feed. Of other creatures frogs are numerous, snakes rare, and mud-fish (*Protopterus*) common.

Draining and the repeated slashing of the vegetation necessary for the protection of the young trees have already caused a number of changes in the status of the fauna (2).

VEGETATION.

1. *The virgin swamp.*

Including the water-lily zone seven plant communities can be recognised:

(1) *Nymphaea* zone. The water-lily community forms a belt 20-50 yards wide separating the swamp from open water. Nine species have been recorded from the belt, of which two, *Ceratophyllum demersum* L. (561¹) and *Utricularia Thonningii* Schumach. (697) are free-floating.

The most characteristic plants in the zone are the blue or pink lilies, *Nymphaea* nr. *Heudelotii* Planch. (500), and *Nymphaea* nr. *zanzibarensis* Caspary. (512), and the sacred lotus, *N. lotus* L. (364), with its sharply toothed leaves and larger white flowers. The other species present are: *Trapa bispinosa* Roxb. (560), *Brasenia peltata* Pursch. (563), *Limnanthemum niloticum* K. and P. (562), and *Ottelia ulvifolia* Walp. (492).

¹ When cited for the first time names are quoted in full as determined at Kew, with the collector's number bracketed. Where determined locally name and authority are given, but no number.

Temperature and rainfall, Kampala, 1930-21.

Month	Dry bulb (° F.)						Mean of daily maximum and minimum (° F.)						Rainfall (in.)		
	1930			1931			1932			1933			1930		
	7th			8.30 a.m.			8.30 a.m.			8.30 a.m.			8.30 a.m.		
	14th	2.30 p.m.	7.50 p.m.	8.30 a.m.	2.30 p.m.	7.50 p.m.	8.30 a.m.	2.30 p.m.	7.50 p.m.	8.30 a.m.	2.30 p.m.	7.50 p.m.	8.30 a.m.	2.30 p.m.	7.50 p.m.
Jan.	62.2	77.5	79.0	70.11	82.4	80.7	80.7	59.2	81.5	66.0	84.4	65.1	2.15	2.82	0.61
Feb.	63.6	80.2	81.7	72.1	80.4	82.3	82.3	60.6	83.5	67.5	82.3	64.8	1.99	0.87	0.72
Mar.	63.5	77.3	76.1	69.5	75.0	80.3	80.3	60.5	79.7	64.4	77.9	62.4	4.61	8.96	10.25
Apr.	63.9	75.9	75.5	68.4	76.5	80.1	80.1	61.2	78.3	64.0	77.6	64.0	5.62	9.96	4.79
May	65.1	76.6	75.8	68.7	73.9	79.6	79.6	61.9	78.3	63.5	76.1	63.0	8.17	5.35	4.81
June	62.4	75.8	74.8	68.1	73.9	79.0	79.0	59.4	77.4	64.0	76.8	62.8	2.58	3.05	0.84
July	62.4	75.6	72.6	65.8	72.0	79.7	79.7	58.1	76.5	62.2	73.0	61.0	2.71	3.77	2.21
Aug.	62.7	76.7	74.6	66.4	74.3	80.5	80.5	58.1	77.9	62.2	77.2	61.3	1.50	1.29	2.20
Sept.	63.3	78.6	74.2	67.3	72.0	81.3	81.3	59.6	79.2	62.2	77.4	61.3	7.71	4.29	6.28
Oct.	63.5	77.9	76.9	69.0	75.4	81.6	81.6	60.1	80.8	63.1	79.5	62.1	4.59	4.88	3.12
Nov.	64.4	79.9	77.2	69.4	76.1	82.8	82.8	60.6	79.9	63.3	79.3	62.1	2.86	6.08	4.73
Dec.	62.7	80.9	76.4	68.6	76.8	83.5	83.5	58.5	79.3	63.5	79.7	62.8	1.57	1.88	4.16
Year	63.3	77.7	76.2	68.6	75.8	80.9	80.9	59.8	79.4	63.8	78.7	62.7	46.06	53.20	44.72

* Figures from *Uganda Protectorate Blue Book* for 1930, 1931 and 1932. Measurements for 1930 taken in the grounds of the Agricultural Department Laboratory, and those for 1931 and 1932 at Kololo Hill. Kampala is roughly 7 miles north-west of Namanve.

Rainfall at Namanve Swamp, June 1932-May 1933.

(Figures for the first 12 months following the installation of a gauge.)		Rainfall (in.)	
Month (1932)	Rainfall (in.)	Month (1933)	Rainfall (in.)
June	1.92	January	2.44
July	2.98	February	3.69
August	2.23	March	7.50
September	5.16	April	4.95
October	6.52	May	3.92
November	6.67	Total for 12 months	50.43
December	2.45		

(2) *Fringing papyrus*. Immediately within the Nymphaea zone is a narrow belt of Papyrus from 5 to 12 yards wide. This belt does not develop *in situ* but owes its origin to wind-borne masses of Papyrus torn during storms from neighbouring swamps. The floating papyrus islands drift through the Lily zone and finally come to rest against the Fern and Sedge Community (see below). In the course of time, by the natural expansion of growth and the addition of fresh masses, a complete fringe is built up.

The dominant plant in the Fringing Papyrus Community is *Cyperus papyrus* L. (381), which attains a height of 9–12 ft. Owing to the constant swell on the lake, and the more violent agitations caused by storms, there is little or no cohesion between individual clumps. One or two small sedges (*Cyperus* spp.), ferns (*Dryopteris striata* C. Chr. (249)), and a very occasional herb (*Dissotis rotundifolia* Triana (232), *Impatiens procridioides* Warb. (382), and *Polygonum* nr. *serrulatum* Lag. (504), recorded), may be found on the peaty bases of the papyrus clumps. From the heavily shaded water between them was collected the duckweed, *Lemna polyrhiza* L. (559).

(3) *Fern and sedge*. The Fern and Sedge Community forms a strip some 20 yards in width between the fringing papyrus and the Limnophyton Swamp. In many lake-shore swamps this community is not found, and at present the factors favouring and limiting its development are not known. In shallow water it can and does arise directly from the Water-Lily Community, and it may possibly only spread over deeper water from such shallow centres.

With the exception of the saw-leaved sedge, *Rhynchospora corymbosa* (L.) Britt. (493), which forms occasional isolated clumps 12 ft. high by 5 or 6 ft. thick, all the plants within the belt are small, rarely over 3 ft. high. From this feature alone the Fern and Sedge is readily picked out from the taller growing communities around it.

The plants forming the belt occur in intimate mixture, their roots so bound together as to form a thin, compact, floating mat of vegetation. When walked upon, this mat sways and sags in a horrible manner beneath one's feet, several square feet at a time disappearing completely below water should one cease moving even for a moment.

The chief species represented here are *Dryopteris striata*, *Pycreus Mundtii* Nees (508), *Pycreus* nr. *Mundtii* Nees (237), *Fimbristylis subaphyllus* Boeckh. (509), *Cyperus Haspan* L. (220), *Leersia hexandra* Sm. (243, 495), *Fuirena pubescens* Kunth. (219), *F. umbellata* Rottb. (460), and *Polygonum* sp. nr. *P. serrulatum*.

(4) *Limnophyton Swamp*. Limnophyton Swamp is a *Cyperus papyrus-Miscanthidium violaceum* Associes in which *Limnophyton obtusifolium* Miq. (501) is subdominant. It is a type of Papyrus Swamp in which the papyrus colonisation is incomplete. *Cyperus papyrus* and *Miscanthidium violaceum* Robyns (217) are the dominant species but the stands are much less dense than in the Papyrus Swamp Community. Open pools and channels up to

30 or 40 sq. yards in extent are common, and on the margins of these pools and scattered through the *Papyrus* and *Miscanthidium* is found the *Limno phyton*. This plant, which is readily recognised by its white flower-spikes and sagittate leaves, is gradually suppressed as *Papyrus* colonisation progresses, and finally disappears as it becomes complete. In some lake-shore swamps, notably around Entebbe, the *Limnophyton* is replaced by a somewhat similar-looking plant, *Caldesia reniformis* Makino (1078). At Namanve the *Limnophyton* Swamp extends from half to three-quarters of a mile inland from the Fern and Sedge belt.

With the exception of the more woody species, the majority of the plants listed below in Table III as occurring in Virgin *Papyrus* Swamp are to be found in the *Limnophyton* Swamp. Because of the much wetter conditions prevailing, their status is, however, different, and it is regretted that it was impossible to determine frequency, owing to lack of time.

From pools in this area were collected *Nymphaea* nr. *Heudelotii*, *Nymphaea* nr. *zanzibarensis*, *Potamogeton Richardi* Solms-Laub. (503), and *Utricularia Thoningii*. On the oozy peat at the pool edges grow *Eleocharis fistulosa* Link. (502), *Xyris capensis* Thunb. (461), and the smaller bladderwort *Utricularia exoleta* R. Br.

(5) *Papyrus Swamp* (*Cyperus papyrus* Consociés). The *Papyrus* Swamp Community occupies by far the greatest part of Namanve. There is here much less exposed water and a much greater accumulation of decaying plant remains above water-level. On this peat many species of herbaceous plants thrive, and, since *Papyrus* does not cast a dense shade, the community is particularly rich in species.

Table I. Frequency of plants in *Papyrus* Swamp Community:

	Under virgin condi- tions	Two years after planting		Under virgin condi- tions	Two years after planting
<i>Cyperus papyrus</i> L.	d.	f.-l.sd.	<i>Rhus glaucescens</i> A. Rich. (sensu lato) (227)	o.	r.*
<i>Miscanthidium violaceum</i> Robyns	f.-a.	f.-a.	<i>Kosteletzkya adoensis</i> Hochst. (221)	o.	o.
<i>Dryopteris striata</i> C. Chr.	f.-a.	f.	<i>Leersia hexandra</i> Sm.	o.	a.-l.sd.
<i>Cissampelos mucronata</i> A. Rich. (210)	f.-a.	o.	<i>Vigna capensis</i> Thunb. (246)	o.	f.
<i>Dissotis rotundifolia</i> Triana	f.-a.	o.	<i>Scleria</i> sp. (244)	o.	a.-l.sd.
<i>Panicum chionachne</i> Mez. (223)	f.-a.	a.-l.sd.	<i>Hyptis Baumii</i> Gürke. (211)	o.	o.
<i>Dryopteris thelypteris</i> A. Gray (216)	f.	o.-f.	<i>Stephania praelata</i> Miers (415)	o.	o.
<i>Fuirena pubescens</i> Kunth.	f.	a.-l.sd.	<i>Melochia melissaeifolia</i> Benth. var. <i>mollis</i> K. Sch. (321)	o.	o.
<i>Ficus umbellatus</i> Vahl. (252)	o.-f.	r.*	<i>Gynura picridifolia</i> Burtt Davy (236, 470)	o.	o.
<i>F. verruculosa</i> Warb. (248)	o.-f.	r.*	<i>Desmodium salicifolium</i> DC. (417b)	o.	o.
<i>Pycreus Mundtii</i> Nees	o.-f.	a.-l.d.	<i>Vernonia dumicola</i> S. Moore (423)	o.	o.
<i>Pycreus</i> sp. nr. <i>Mundtii</i> Nees	o.-f.	a.-l.d.	<i>Ethulia conyzoides</i> L. (424)	o.	o.
<i>Rubus rigidus</i> Sm. (209)	o.-l.f.	r.*	<i>Hibiscus diversifolius</i> Jacq. (239) fls. yellow	o.	r.
<i>Myrica Kandtiana</i> Engl. (207)	o.-l.f.	r.*	<i>H. diversifolius</i> Jacq. (322) fls. purple	r.	r.
<i>Fuirena umbellata</i> Rottb.	o.	f.-a.	<i>Sesbania Dummeri</i> Phill. et Hutch. (425)	r.	r.
<i>Lissoschilus paludicolus</i> Rehbr. f. (206)	o.	o.†	<i>Cissus Oliveri</i> Gilg. (254)	r.	r.
<i>L. porphyroglossus</i> Rehbr. f. (201a)	o.	o.†	<i>Trichopteryx flammida</i> Benth. (418)	r.	r.
<i>Typha latifolia</i> L. (247)	o.	o.†	<i>Lissoschilus Wilsoni</i> Rolfe (292)	r.	r.
<i>Syzgium cordatum</i> Hochst. ex Sond. (229)	o.	r.*	<i>Cyperus latifolius</i> Poir. (435)	r.	r.
<i>Bridelia micrantha</i> Baill.	o.	—	<i>Oldenlandia macrophylla</i> DC. (505)	r.	o.
<i>Polygonum serrulatum</i> Lag. (218)	o.	r.	<i>Lygodium scandens</i> Sw. (467)	r.	—
<i>Torenia parviflora</i> Ham. (251)	o.	o.	<i>Impatiens proceridioides</i> Warb.	r.	o.
<i>Tristemma leiocalyx</i> Cogn.? (240)	o.	o.	<i>Triumfetta macrophylla</i> K. Sch. (380)	r.	r.
<i>Cissus adenocaulis</i> Steud. ex A. Rich. (238)	o.	r.	<i>Eulophia alta</i> Fawcett et Rendle (430)	r.†	r.†
<i>Oldenlandia goreensis</i> (DC.) Summerh. (241, 247)	o.	o.	Moss (320)	l.a.	l.f.
<i>Cyperus Haspan</i> L.	o.	a.-l.d.			
<i>Mikania scandens</i> Willd. (245)	o.	o.			

* Dying.

† Not flowering.

‡ Local.

Of the plants listed above, *Cissus*, *Cissampelos*, *Mikania*, and *Lygodium* climb on the Papyrus stems, *Rubus rigidus* is a Rambler, and *Vigna capensis* a scrambler. The *Ficus* and the *Bridelia* are woody species which on drier sites may attain 25 ft. in height. In the swamp they never exceed 12 ft. *Rhus*, *Myrica*, and *Sesbania* are shrubs. *Syzygium cordatum* is the only species which overtops the papyrus: it is usually gregarious, and may reach 20 ft.

(6) *Miscanthidium Swamp* (*Miscanthidium violaceum* Consociates). The *Miscanthidium* Community is found in isolated patches scattered throughout the drier and older portions of the Papyrus Swamp. These patches, which vary from a few square yards to several acres in extent, appear to coincide with areas where the underlying clay beds are nearer the water surface than is the case beneath the Papyrus. In the course of time, owing to the natural elevation of the swamp through the gradual accumulation of peat, the patches are constantly enlarging.

In swamps surrounded by grass or scrub-lands *Miscanthidium Swamp* is a stage nearer the climax community of Tropical Rain Forest than is Papyrus Swamp. Succession proceeds from Papyrus Swamp direct through *Miscanthidium Swamp* to the many stages of Grassland and Scrub, and by further stages, to Forest. Where, as at Namanve, the swamp is already completely surrounded by forest, development through Grassland does not take place and the *Miscanthidium Swamp* is then only an additional stage in the otherwise direct development of Papyrus Swamp to *Phoenix Swamp* and thence to Forest.

The surface of the ground in *Miscanthidium Swamp* is much more level than in the case of Papyrus Swamp. In addition, the roots of the *Miscanthidium* form a firm, compact mat and there is none of the soft blackish ooze found below Papyrus. The grass forms dense stands 8–12 ft. high, and casts a heavy shade, often aggravated by the flattening of the stands by wind. In this shade few plants can exist so that the number of species present in the community is small.

Table II. *Frequency of plants in Miscanthidium Swamp Community:*

	Under virgin condi- tions	Two years after planting		Under virgin condi- tions	Two years after planting
<i>Miscanthidium violaceum</i>	d.	f.-a.	<i>Rhus glaucescens</i>	o.	—
<i>Dryopteris thelypteris</i>	o.-l.f.	r.	<i>Scleria</i> sp.	o.	a.
<i>Cyperus papyrus</i>	o.	r.	<i>Otomeria dilatata</i>	o.	f.
<i>Dryopteris striata</i>	o.	a.	<i>Dissotis incana</i>	o.	f.
<i>Cissampelos mucronata</i>	o.	r.	<i>Lygodium scandens</i>	r.	r.
<i>Panicum chionachne</i>	o.	f.-a.	<i>Hyptis Baumii</i>	r.	r.
<i>Ficus verruculosa</i>	o.	r.*	<i>Satyrium niloticum</i>	r.	f.
<i>Pycereus Mundtii</i>	o.	a.-sd.	<i>Ophioglossum cf. lancifolium</i>	r.	f.
<i>Pycereus nr. Mundtii</i>	o.	a.-sd.	<i>Eulophia alta</i>	r.†	r.†
<i>Syzygium cordatum</i>	o.	—	Moss (320)	l.a.	l.a.
<i>Oldenlandia goreensis</i>	o.	f.			

* Dying.

† Local.

Whilst many species which occur in Papyrus Swamp are not found in *Miscanthidium Swamp*, there are only four species found in the *Miscanthidium*

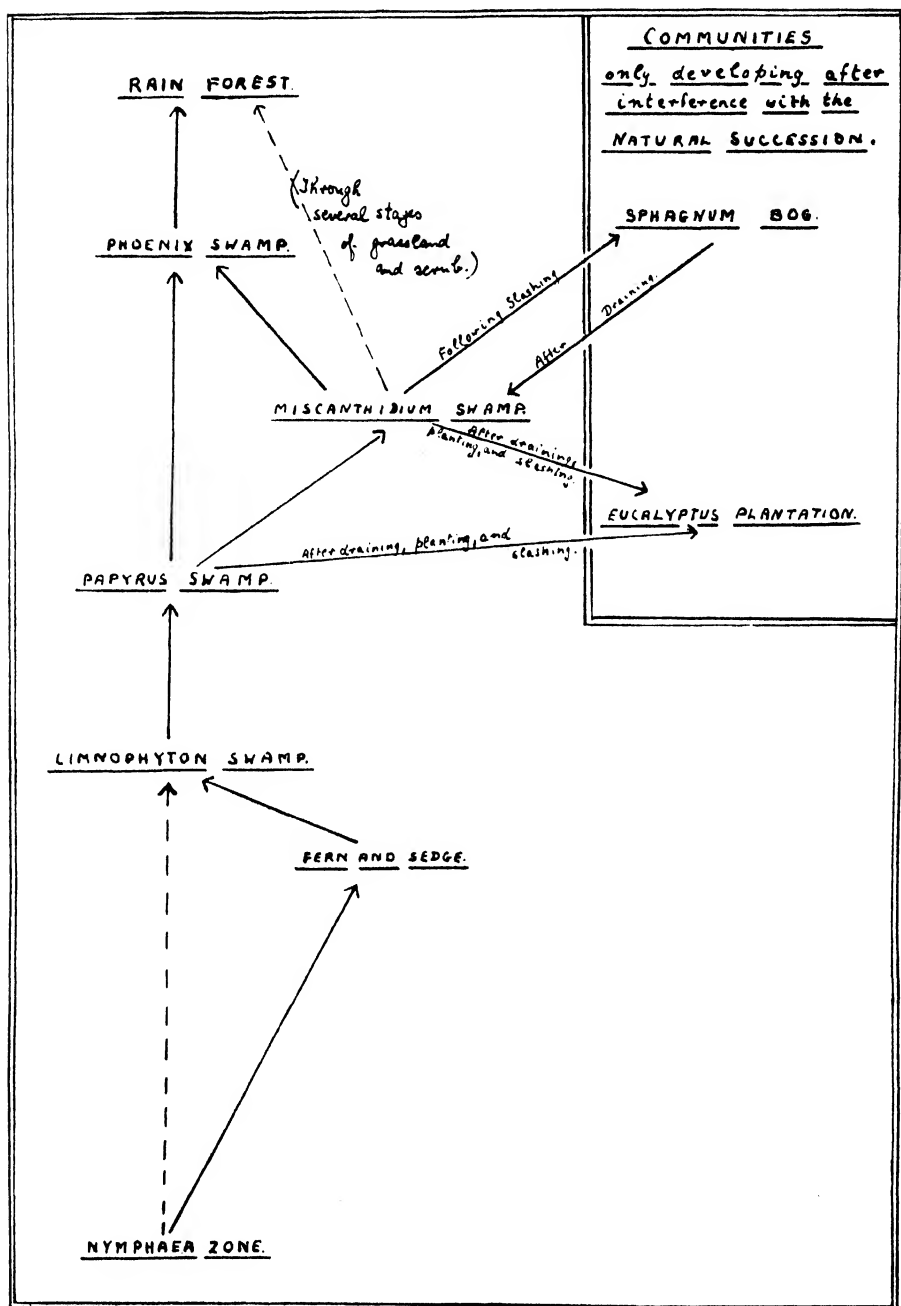


FIG. 2. Chart to illustrate swamp succession. (Bold lines show stages to be seen at Namanve.)

which do not occur in the Papyrus. These are *Ophioglossum* sp. (cf. *O. lancifolium* Pr. (476), *Otomeria dilatata* Hiern. (234), *Dissotis incana* Triana (242), and the orchid, *Satyrium niloticum* Rendle (291)).

(7) *Phoenix Swamp*. Separating the Papyrus and *Miscanthidium* Swamp Communities from the surrounding forest is a narrow belt of Phoenix Swamp. This is the "Swamp Forest" pictured by Troup in (3). The belt is generally some 20 yards in width, except where a stream passes through, when it widens out to follow the banks of the stream inland.

The vegetation is characteristic. It consists in the main of water-loving, woody species with an average height of 20-30 ft. The chief of these are wild date palms (*Phoenix reclinata* Jacq.), *Voacanga obtusa* K. Sch., *Ficus umbellatus*, *Syzygium cordatum*, *Mitragyna stipulosa* O. Ktze., and, where the swamp merges into forest, raphia palms (*Raphia monbuttorum* Drude.), an occasional *Pachystela* (probably *P. brevipes* Baill.), *Erythrina* sp. nr. *E. excelsa* Bak., the common *Pseudospondias microcarpa* Engl., usually heavily buttressed at the base, and a few *Parkia filicoidea* Welw. A white-flowered swamp *Acacia*, probably *A. Mildbraedii* Harms. (441), occurs sparingly in places.

Below the woody species the floor consists mainly of bare, slimy mud and open, shallow pools. On the side remote from the forest, where side-light enters is an undergrowth consisting chiefly of *Cyperus papyrus* or *Miscanthidium violaceum* with a few shrubby species such as *Alchornea cordifolia* Müll. Arg. (344), *Neoboutonia Melleri* Prain (388), *Triumfetta macrophylla*, and *Hibiscus diversifolius*. *Cissampelos mucronata* and *Vigna capensis* are the commonest creepers.

Deeper in the belt and as the shade increases all the above species disappear giving place to scattered *Clinogyne ugandensis* K. Sch. (398), and *Clinogyne* sp. (397), with occasional *Leca guineensis* G. Don., and *Costus afer* Ker. On approaching drier ground there is a rapid transition to a reduced type of Rain Forest.

II. *The drained swamp.*

Of the seven types of swamp listed above, only those dealt with in the greatest detail, namely Papyrus Swamp and *Miscanthidium* Swamp, so far bear a plantation crop. Drained *Phoenix* Swamp is also likely to be suitable for planting and work on a portion of it at the northern end of Namanve is shortly to commence. With regard to the other communities, these are too near the Lake for planting ever to be possible.

The changes which occurred in the Papyrus and *Miscanthidium* areas during the first year of treatment appeared to be due far more to the repeated slashing of the vegetation necessary to protect the young Eucalyptus than to the effects of drainage.

Thus in the Papyrus Swamp, which always contained a large variety of species, the first changes to be noted were the disappearance of some plants

and the increased spread of others, rather than the arrival of new species. During the next twelve months, however, fresh plants began to appear, and when these were recorded it was from areas where the results of draining were most noticeable, and such species were generally well-known pioneers. It is anticipated that, as work proceeds, the effect of the prolongation of the centre drain will have made itself felt in the last few compartments before they are cut over for the first time, and here one would expect the changes due to light ingress and to the appearance of pioneer species to take place simultaneously.

Drained Papyrus Swamp. Taking the Community as a whole, *Cyperus papyrus* is still the commonest species, but is gradually becoming suppressed through continued cutting back. The chief reaction has been the greatly increased spread of the grasses and sedges, all those recorded from the Virgin Swamp becoming abundant, locally subdominant, or even, over small areas, locally dominant, and in the almost immediate suppression of the woody species such as *Rhus*, *Myrica*, *Syzygium* and *Ficus*. On the drier areas, there has been a great spread of the yellow-flowered *Vigna capensis*.

It is obvious that this state of affairs is going to be of short duration, and as soon as the Eucalyptus begin to get properly under way, the sedges, at any rate, are bound to become quickly suppressed. Already, at the time of writing, 29 months after planting, the early planted areas appear as if they would shortly contain little else than a tree crop of *Eucalyptus robusta* with a ground cover of an Umbellifer, *Oenanthe palustris* (Chiov.) Norman (494), which was never recorded from the Virgin Swamp (Pl. XXXIV, phot. 9).

The other species which have appeared in this table since reclamation began are listed below:

Table III. *Plants appearing in Papyrus Swamp following draining and afforestation.*

	Frequency after planting			Frequency after planting	
	18 months	24 months		18 months	24 months
<i>Oenanthe palustris</i>	o.	f.-l.d.	<i>Asclepias semilunata</i> N.E.Br. (323)	Vagrant	—
<i>Hydrocotyle monticola</i> Hook f. (451)	r.	o.-l.f.	<i>Mimosa asperata</i> L.	—	o.
<i>Bidens pilosa</i> L. (507)	r.	o.	<i>Oldenlandia lancifolia</i> Schweinf. (450)	—	o.
<i>Gynura vitellina</i> Benth.	r.	o.	<i>Melanthera Brownei</i> Sch. Bip. (466)	—	r.
<i>Aspilia latifolia</i> Oliv. and Hiern.	r.	o.	<i>Ludwigia prostrata</i> Roxb. (497)	—	r.
<i>Buchnera capitata</i> Benth. (452)	r.	r.	<i>Commelina nudiflora</i> L. (454)	—	r.
<i>Alectra communis</i> Hemsl. (453)	r.	r.	<i>Eucalyptus robusta</i> Smith (planted)	(6 × 6 ft.)	(6 × 6 ft.)

Drained Miscanthidium Swamp (Pl. XXXIII). Although a number of species, excluded from the Virgin *Miscanthidium* Community because of the density of the shade, soon begin to appear once the stands are cut over, the chief response to the increase of light is again in the great spread of the grasses and smaller sedges. These plants, together with the fern *Dryopteris striata*, none of which were more than occasional in the untouched swamp, quickly become exceedingly abundant and, in places, co-dominant with the *Miscanthidium*. The



Phot. 6. Drained *Miscanthidium* Swamp, showing *Olomeria dilatata*,
(*Cynorchis anacamplodes*, and *Habenaria* sp. nov.



Phot. 5. Drained *Miscanthidium* Swamp. *Satyrion ulotectum*
amongst *Miscanthidium violaceum* (with white midribs) and
Dryopteris striata.

latter, after two years of repeated cutting back, is often no more than frequent, where formerly it was dominant. Just as in the case of the Papyrus Swamp, all woody species and twiners rapidly vanish, whilst another striking feature is the almost complete disappearance of *Dryopteris thelypteris*, which prefers the cool, dark conditions of the uncut stands.

Amongst swamp-loving new-comers may be mentioned the sedges *Leersia hexandra*, *Fuirena pubescens* and *Cyperus Haspan*, and the three orchids, *Cynorchis anacamptoides* Kraenzl. (455), with small spikes of pinkish-purple flowers, *Nervilia afzelii* Schltr. (1453) with single, drooping white flowers, and a new species of *Habenaria* (290), not yet named. As with *Dissotis incana*, *Ophioglossum*, *Satyrium*, *Otomeria*, and the four species listed below as occurring in Sphagnum patches, none of these three orchids have so far been found at Namanve from outside *Miscanthidium* areas.

It will be seen on comparing Tables III and IV that of the several dry ground plants, which are present in the Papyrus community after two years of draining, only one, *Gynura picridifolia*, is found in the drained *Miscanthidium*, although the latter community contains three species, *Helichrysum cymosum* Less. (226), *Sopubea ramosa* Hochst. (462), and *Blumea lacera* DC. (258), not recorded from the drained Papyrus.

Miscanthidium Swamp is capable of holding up water to a greater extent than Papyrus Swamp, and a correspondingly longer time elapses before draining takes effect. After two years the surface peat is only just becoming dry, and the pioneer plants, which by this time are reasonably common in Papyrus areas, are only beginning to find a footing in the *Miscanthidium*.

It is extremely doubtful if it will ever be possible to raise a plantation crop on *Miscanthidium* areas, unless they can be completely dried out and intensively cultivated. The trees are difficult to establish, and grow badly, mainly owing to the small quantity of dry soil available. After two years even the best of them are barely 3 ft. high, which compares very unfavourably with 18 ft. at a similar age in Papyrus Swamp.

Table IV. *Plants appearing in Miscanthidium Swamp following draining and afforestation.*

	Frequency after planting			Frequency after planting	
	18 months	24 months		18 months	24 months
<i>Nervilia afzelii</i>	f.	f.	Pioneer species:		
<i>Habenaria</i> sp. nov.	l.f.	l.f.	<i>Gynura picridifolia</i>	—	r.
<i>Cynorchis anacamptoides</i>	o.	o.	<i>Sopubea ramosa</i>	—	r.
<i>Cyperus Haspan</i>	o.	l.f.	<i>Blumea lacera</i> (var.)	—	r.
<i>Fuirena pubescens</i>	o.	l.f.	<i>Helichrysum cymosum</i>	—	r.
<i>Leersia hexandra</i>	o.	l.f.	Plants of the Sphagnum Society:		
<i>Torenia parviflora</i>	r.	r.	<i>Sphagnum Franeonii</i> Warnst. (458)	l.f.	l.f.
<i>Eucalyptus robusta</i> (planted)	(6 × 6 ft.)	(6 × 6 ft.)	<i>Lycopodium carolinianum</i> L. (457)	o.	o.
			<i>Drosera madagascariensis</i> DC. (459)	r.	r.
			<i>Disa Emdinii</i> Kraenzl.	—	r.

In the first two compartments to be planted at Namanve the opening up of the *Miscanthidium* Swamp led to the formation of tiny patches of a Sphagnum Society, whose appearance was first noted some sixteen months after the first slashing down of the vegetation. This Society, from which only four species were recorded, developed in small damp depressions, the largest of which was under 4 sq. ft. in area. As soon as the effect of drainage began to make itself felt these depressions dried out, and the plants disappeared. Twenty-nine months after the first slashing no trace of the community remained. The commonest member of the society was a species of *Sphagnum* moss, *S. Franeonii*, amongst which could usually be found the club moss, *Lycopodium carolinianum*. In some, but by no means all of the patches, occurred a pretty pink-flowered sundew, *Drosera madagascariensis*, and from one was collected *Disa Eminii*, an orchid with vivid red flowers.

It appears likely that at low altitude at any rate the Sphagnum Community only develops where the natural succession is upset. Further examples of its occurrence were examined at Luzira Swamp, near Port Bell, not far from Namanve, and on a marshy strip of ground, which separates Lake Nabugabo in Masaka district from Lake Victoria. In both areas the community has arisen in annually burnt *Miscanthidium* Swamp (i.e. in swamp where the fire factor has allowed the entrance of light just as slashing has allowed it at Namanve). At Luzira, where the practice of burning the swamp is of recent date, the Sphagnum patches are still small, and very similar to those at Namanve. An additional species, *Utricularia subulata* L. (569), occurs here, but the *Disa* is absent.

At Nabugabo the fishermen who frequent the swamp are reputed to have burnt it annually for a long period. Owing to the situation, there is no possibility of desiccation even in the most abnormal season, and conditions are ideal for the development of the community. The patches at Nabugabo attain several acres in extent: Sphagnum is dominant and tufts of reeds and grasses scattered amongst it. In 2 hours spent here in January 1933 the following species were collected growing intimately with the moss:

Sphagnum macromolluscum Dix, sp. nov.

Ms. (571)

Lycopodium carolinianum

Drosera madagascariensis

Disa Eminii Kraenzl.

Utricularia subulata

Utricularia appendiculata Bruce sp. nov.

Ms. (585)

Monechma subsessile C.B. Cl. (572)

Syngonathus sp. (573)

Pycnosphaera Buchananii N.E.Br. (574)

Ascolepis capensis Ridley (583)

Mesanthemum radicans Koernicke (580)

Otiophora pycnostachys K. Sch. (582)

Xyris sp. (584)

Crassula sp. nr. *C. alsinoides* Engl. (587)

Phaius occidentalis Schltr. (588)

Abundant. Not at Namanve or Luzira

Common. Present at Namanve and at Luzira

Common. Present at Namanve and at Luzira

Locally common. Present at Namanve but not at Luzira

Common. Not present at Namanve but present at Luzira

Fairly common, twining on Grass stems. Not present at either Namanve or Luzira

Not present at either Namanve or Luzira

Do.

Do.

Do.

Do.

Do.

Do.

Do.

Do.



Phot. 7. *Eucalyptus robusta* 18 months after planting. Flooded ditch in foreground.



Phot. 8. *Eucalyptus robusta*, 36 months after planting. The trees on the right are the same as those in Phot. 7.



Phot. 9. 3-year-old swamp-planted *Eucalyptus*, showing characteristic ground cover of *Oenanthe palustris* and scattered shrubby *Triumfetta macrophylla*.

Coleus sp. cf. <i>C. darfurensis</i> R. Good (578)	Not present at either Namanve or Luzira
<i>Polygala filicaulis</i> Baill. (576)	Do.
<i>Dissotis incana</i>	Do.
<i>Dissotis Trothae</i> Gilg. (577)	Do.
<i>Vausagesia africana</i> Baill. (581)	Do.

Ditch vegetation. Owing to periodic cleaning little vegetation is allowed to develop on the drainage ditches at Namanve. Here and there, however, where trailing grasses or fallen Papyrus stems form some slight obstacle to surface flow one may find a water cover of *Pistia stratiotes* L. (506), *Ricciocarpus natans* Corda (499), and *Lemna gibba* L. These three plants develop with amazing rapidity, all the *Pistia* at Namanve being derived from four rosettes, which drifted down to it in 1931 from the overflow of a native well. In addition to the above, *Ottelia ulvifolia*, and *Utricularia exoleta* can be found where the ditch edges are soft and oozy, whilst on the banks, hanging down over the water, grow *Hydrocotyle asiatica* L. (510), *H. bonariensis* L. (511) and *H. monticola*, the last named of which may extend back for some distance into the drained Papyrus Swamp.

SUMMARY.

1. A description is given of a tropical swamp in process of afforestation with *Eucalyptus*.
2. The vegetation of the swamp under virgin conditions is dealt with community by community. Greatest attention is paid to the *Cyperus papyrus* and *Miscanthidium violaceum* Consociates, which are those most affected by reclamation.
3. The changes which have taken place in the vegetation during the first two years of the reclamation scheme are indicated.

ACKNOWLEDGMENTS. The great majority of the plants cited above were forwarded to the Royal Botanic Gardens, Kew, for identification. The writer takes great pleasure in acknowledging his gratitude to the Director, to the Staff of the African Section of the Herbarium, and, more especially, to Dr A. D. Cotton, Keeper of the Herbarium for their assistance. In addition to a complete set of specimens deposited at Kew, duplicates of most of the numbers have been lodged in the Forest Department Herbarium, Entebbe.

The writer also wishes to record his thanks to Maurice Kanya, Deputy Native Ranger in the Uganda Forest Department for help in the field, and to Mr G. L. R. Hancock, Assistant Entomologist in the Agricultural Department, for assistance generally.

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AN UNGRAZED GRASSLAND ON LIMESTONE IN WALES, WITH A NOTE ON PLANT "DOMINIONS"

By R. C. McLEAN.

(With two Figures in the Text.)

ON the south coast of Wales the Gower peninsula juts out some 23 miles due westward into the Bristol Channel. Although the mainland is an industrial area and densely populated, the peninsula itself is purely agricultural, has no railway and is thinly populated, with large areas of natural vegetation. At the western extremity stands Worm's Head, a rocky islet, rather more than 1 mile long, cut off at high tide by rather more than one-third of a mile of sea.

This insulated promontory consists of four small hills in line, of which the highest is not more than 200 ft. above high-water mark. The outermost rears up precipitously to form the head of the "Worm", while the rounded outlines of the other three represent the convolutions of its body; the whole being a well-known landmark to shipping in the Bristol Channel. Fig. 1, which is an outline map of the area, illustrates this description.

The rock of the headland itself and of the neighbouring mainland, is Carboniferous limestone of lower zones, which abuts about 2 miles north-east on to a Devonian conglomerate. The dip is steeply south-south-west. The low hills are partly rocky and partly covered by calciphile grassland, and it is the remarkable difference between the grassland on the Outer and Middle Headlands and that on the Inner Headland and the mainland adjacent, which prompts this note.

In Fig. 2 are shown the profiles of the four hills or articulations of the "Worm", successively, in section north to south. It should be noted that the exceptional tide range of the Bristol Channel (40 ft. and over) leaves a wide fringe of rocky foreshore on the south side at low tide and a broad belt of exposed rock connecting the Inner Head to the mainland.

The grassland of the Inner Head is essentially the same as that on the mainland, and the same description will apply to both. Both are heavily grazed by sheep. The covering of the lower slopes is lush and well grown, but in ascending the vegetation becomes dwarfer and more turfy in character, finally tailing out on to bare rock at the summit, with an increasing predominance, as one ascends, of the rock-loving species marked "rk." in the list on p. 439.

The lower soil slopes are covered to a depth of 2-6 ft. with a ferruginous loam, a talus soil, derived erosively from the limestone but practically non-

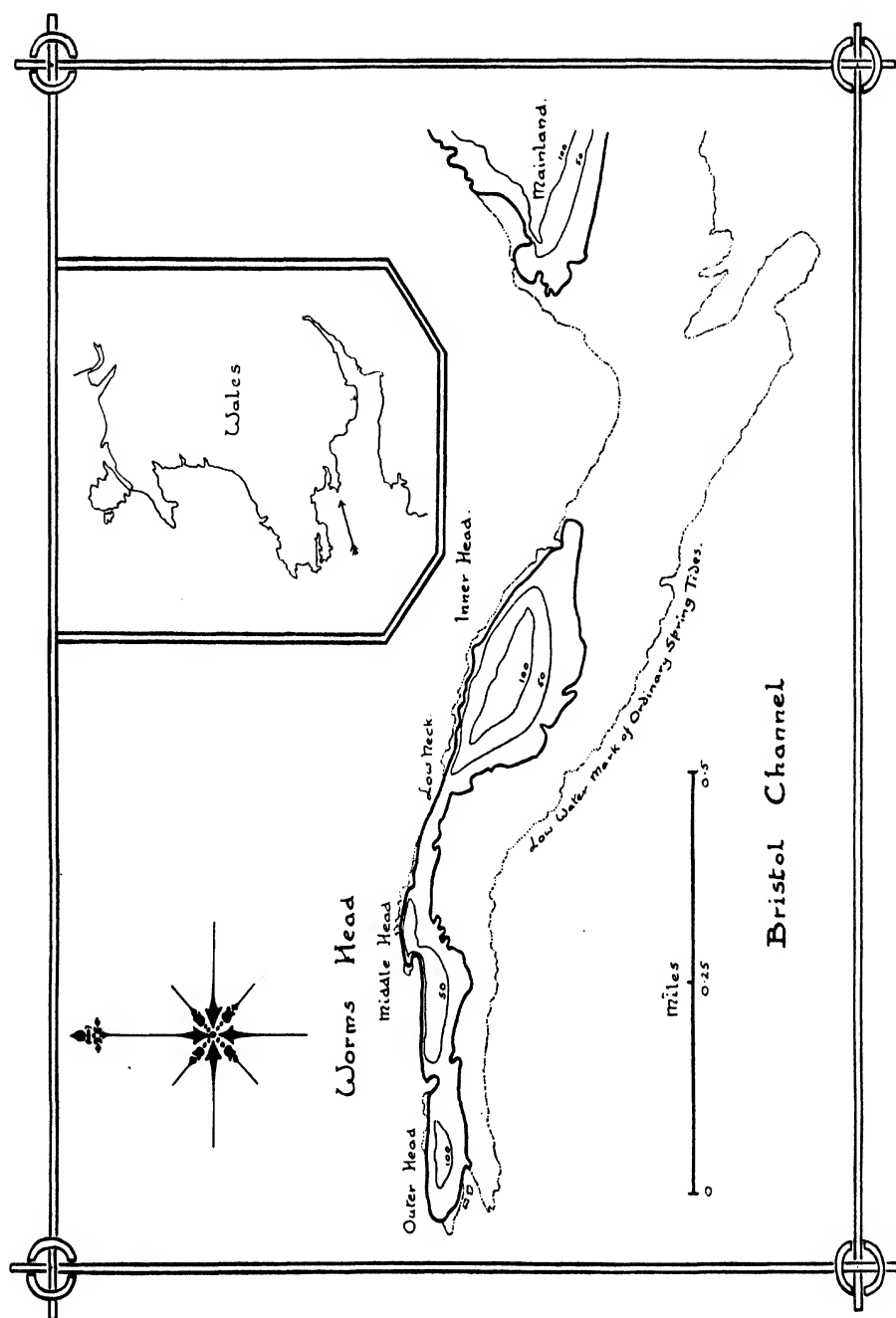


FIG. 1. Outline map of the Worm's Head reduced from the scale of six inches to the mile, showing the belt of tidal rocks that connects it to the mainland (Gower). Inset: an outline of Wales; position of the area indicated by an arrow.

calcareous, the CaCO_3 having been leached out during, and after, the subaerial formation of the soil. This talus is exactly similar in character to the soil which forms above the limestone cliffs of the mainland, and which bears a heath association characterised by *Ericaceae*, *Ulex Gallii*, and *Molinia coerulea*, even, in parts, within a few inches of the underlying limestone. It is, in fact, the insoluble residue from the weathering of the limestone, having the heavy texture, low humus content, low water content and high ferric coloration with downward enrichment, which characterise the Reef Type of Terra Rossa developed on calcareous rocks in Central and Southern Europe. Similarly, the dark, alkaline (pH 7.2–7.8) soils of the surface pockets of the limestone are practically Black Earth reef-soils such as occur, also on calcareous substrata, in the Jura of Southern Germany.

These are not of the true, arid Black Earth type of Eastern Europe, but are to be distinguished under the general Polish name of Rendzina, according to Ramann (1928).

The existence of these two climatic soil types in Britain, even in small expanses, has not been previously suggested. It is not unlikely that other European soil types with well-marked climatic relationships may be found to have unexpected extensions north-westward to our shores.

We are dealing here with an area which is south of the margin of maximal glaciation, so that the red soil is a sedentary and probably a very old one. Its recognition must, indeed, affect the accepted estimate of the probable glaciation of this coast, since it is very unlikely that the thickness of limestone whose erosion has left these red-soil residues could have been removed since the close of the ice-age. The deposits have possibly been accumulating continuously since the close of the Tertiary, inasmuch as they lie, in part at least, above the reach of the post-glacial fluctuations of sea-level.

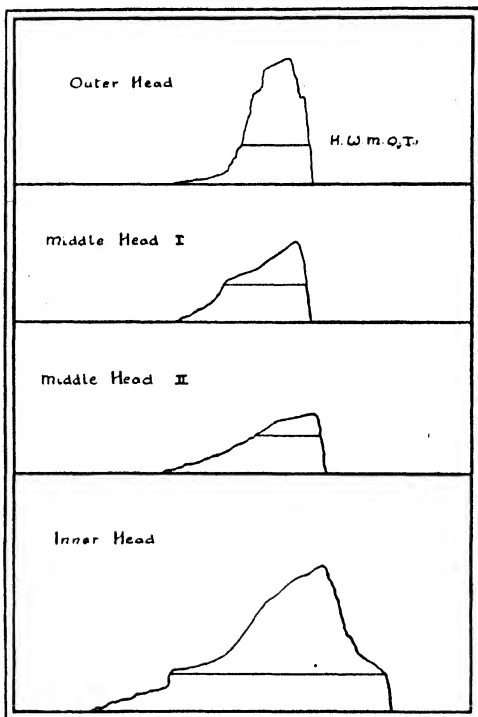


FIG. 2. Profiles from north to south of the four articulations or segments of Worm's Head, arranged on a common axis. The vertical scale is 8.5 times the horizontal. The horizontal line across each profile shows the high-water mark of ordinary tides (H.W.M.O.T.). The *Festucetum* covers the sinistral slope of the two portions of the Middle Head.

The sheep which graze this (inner) part of the Headland tend to congregate on the upper ledges, where they find wind-breaks, and here is a "lair-flora" characterised by the species marked "lf." in the accompanying list.

Grasses

<i>Festuca ovina</i>		<i>Holcus lanatus</i>	
<i>Agrostis vulgaris</i>		<i>Cynosurus cristatus</i>	
<i>Poa pratensis</i>		<i>Poa annua</i>	lf.
<i>Dactylis glomerata</i>	lf.		
<i>Erica cinerea</i>		<i>Poterium Sanguisorba</i>	rk.
<i>Calluna vulgaris</i>		<i>Bellis perennis</i>	lf.rk.
<i>Ulex Gallii</i>		<i>Pieris hieracioides</i>	
<i>Rubus rusticanus</i>		<i>Leontodon hirtus</i>	
<i>Trifolium repens</i>		<i>Potentilla erecta</i>	
<i>Lotus corniculatus</i>	lf.rk.	<i>Galium verum</i>	rk.
<i>Plantago lanceolata</i>		<i>Cerastium vulgatum</i>	lf.
<i>P. maritima</i>	rk.	<i>Rumex Acetosa</i>	lf.
<i>P. Coronopus</i>	lf.rk.	<i>Cirsium lanceolatum</i> (occ.)	
<i>Armeria maritima</i>	rk.	<i>Viola Riviniana</i>	
<i>Sedum acre</i>	lf.rk.	<i>Spiranthes autumnalis</i>	
<i>Thymus Serpyllum</i>	rk.	<i>Medicago lupulina</i> (rare)	

Fairy rings of *Marasmius oreades*, abundant.

This miscellany may be taken as characteristic of these limestone grasslands wherever they are subject to grazing.

Reference to Fig. 1 will show, however, that there is a low belt of rock between Inner Head and Middle Head, which descends almost to high-water mark and is extremely broken and rugged. The sheep on Inner Head do not cross this, so that all the vegetation beyond is permanently free from their influence. The Outer Head is too precipitous for anything but chomophytes, but on Middle Head and Low Neck there is a grassland of peculiar character, which contrasts most strikingly with the grazed pasture of Inner Head, only a few hundred yards distant, although growing under closely similar conditions in all respects except in regard to grazing.

Here we have a slope, fully exposed to the prevalent south-westerly winds which come in unstayed from the Atlantic; a slope not rising at its highest above 50 ft. from high-water mark, which bears, instead of the close stunted turf that is almost universally characteristic of such situations, a deep, soft carpet of luxuriant grass. It is, in fact, not so much a carpet as a mattress, through which, in places, a stick may be thrust down for a couple of feet before it touches the soil.

The dominant grass is *Festuca rubra*, subspecies *eu-rubra* var. *genuina*, subvariety *pruinosa* Häckel¹, and over most of the area it is perfectly pure. It flowers freely and its leaves are over 1 ft. long. Here and there are patches with an admixture of *Dactylis glomerata* and *Holcus lanatus*, but such associates as occur are to be found chiefly as isolated plants, of large size, half-buried amid the dominant *Festuca*.

These associated species, arranged more or less in order of frequency, are as follows:

¹ I am indebted to Mr W. O. Howarth, of Manchester University, for the determination.

Beta maritima
 Silene maritima
 Rumex Acetosa
 Trifolium repens
 Armeria maritima
 Sonchus oleraceus
 Rumex crispus

Plantago lanceolata
 Limonium binervosum
 Cirsium lanceolatum
 Spergularia rupestris
 Leontodon hirtus
 Galium verum (occ.)

The underlying soil is, as the above list indicates, rich in humus. The Inner Headland is manured by both sheep and sea-birds, this area by sea-birds alone. Their droppings are full of fragments of mussel shells, which also abound in the soil. Hence comes an average humus content of 15.1 per cent. of dry soil-weight and a calcium carbonate content of 4.25 per cent. The reaction is alkaline (pH 7.8) and the texture colloidal, binding readily under pressure. It is also full of ants.

I wish to emphasise that the whole area is visited by flocks of birds, and that the great differences in vegetation and soil between one part and another seem to be attributable to the presence or absence of the sheep alone.

Davies, in *Bull. Welsh Plant Breeding Station*, Ser. H, No. 8, 1928, remarks that red fescue is generally a non-aggressive species in competition with other pasture grasses, but tends, with the passage of time, to make recovery by vegetative means.

The fescues in general are particularly sensitive to competition by species which are less injured by grazing; grass species being aggressive in well-established pastures in proportion to their ability to withstand heavy grazing. In very poor ground root competition may also be important and the fescues are deep-rooted, which tells against them on shallow soils.

It is almost needless to comment on the remarkable effects a grazing barrier may have on vegetation, since so many examples are well known. So far as this region is concerned, the moral of this natural enclosure experiment appears to be that the short, grass pasture of exposed limestone, which occupies a considerable area in Great Britain, is probably of the nature of a subclimax, in Clements' sense, controlled by biotic rather than climatic influences and that the true climax of limestone grassland is a long-grass Festucetum. This supports the view, held by Clements, that the short-grass prairie of North America is a grazing subclimax and that the true climax of the Great Plains area is a mixed long-grass.

NOTE ON PLANT "DOMINIONS".

The *Festuca rubra* community described above illustrates a concept which the author has found valuable as a means to clearer apprehension of the relations involved in some types of community.

There are many plant groupings in which a single species so completely dominates the ground that the conditions upon which its associated species depend are essentially due to the presence and growth of that species. It is to such types that the term "dominion" seems more applicable than "associa-

tion", for there is not here the condition of community based upon co-relationship to a set of natural conditions which seems to be the essential meaning of the latter term.

In the cases indicated as dominions the relationship expressed is one of self-sufficiency on the one hand and complete dependence on the other. Wherever the sociological condition is one of monarchy, there is a plant "dominion". Where, on the other hand, the ecological status of a number of associates is uniform, there is "communion".

More than one form of society comes into this concept. There is, for example, the grouping where the monarch and subject species are of such different habit and life-form that the only effective biological relation between them is the unilateral impact of dominant on subordinate, as in the case of a natural pine forest and its ground vegetation. There are also cases, such as the present example, where the subject plants are of the same biological status as the monarch but are nevertheless ecologically dependent upon its existence just as truly as if they were its parasites. In both cases one might indeed say that the subject species are ecological parasites of the monarch species. Were it to disappear they must perforce follow suit. That is the essence of the dominion.

Where the same relations obtain, but the determining influence is exercised, not by a single monarch species, but by a couple or more of truly "associated" species, the whole community is best regarded as a "condominion". Thus widened the concept covers a considerable percentage of the communities usually called associations. The only excuse for introducing a new term in Ecology is that it makes for greater clarity by a truer expression of relationship. This plea may perhaps be allowed in the present instance.

Dominance has, of course, been frequently employed before in analysing the concept of association. Katz (1930) showed that throughout the communities of Northern and Eastern Europe, ranging from sphagnalean-herb-grass groupings to *Cladonia*-rich heaths and mossy needlewoods, there is a very high, probably a predominant number of species whose constancy is regulated by the dominant species and changes quantitatively with the changes of the dominants. To prove this, however, Katz has recourse to an analysis of each association into layers, within which dominant and subordinate species are quantitatively related and this to him is the essential structure of a true association.

Similar views of dominance as the criterion of association individuality have been expressed by Warén and Cajander (1926), Lüdi (1928), du Rietz (1926) and Sukachev (1929), though such a concept by itself is generally felt to be inadequate.

Subordinate species which change quantitatively along with dominants may really be co-dependent on some external factor which influences both directly, each in its degree. That is true association, not dominion and the latter idea contains no element of such definitely quantitative relationship.

Furthermore, it seems illogical to treat layers of a community as distinct entities in order to fit them into a scheme of classification. The oak and ash in a Liassic marl woodland may possibly be considered together as a true case of association, while the lower layers are separately considered as secondary associations, but it is impossible to overlook the fact that the community also forms a factorially integrated "whole" and is best treated as such under the heading of a condominium.

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THIRD REPORT ON THE TRANSPLANT EXPERIMENTS OF THE BRITISH ECOLOGICAL SOCIETY AT POTTERNE, WILTS.

By ERIC M. MARSDEN-JONES AND W. B. TURRILL.

(With one Figure in the Text.)

SINCE the preparation of the second report (December 1931) the committee has met at Potterne and made a detailed inspection of the plots. General approval was expressed of the conduction of the experiments for 1932-3.

The results obtained with three additional plants—*Fragaria vesca* and *Phleum pratense*, "diploid" and "hexaploid"—are recorded here for the first time.

The preliminary experiments with *Solanum dulcamara* L. var. *marinum* Bab. and *Bellis perennis* L. suggested that these plants would not be satisfactory for the Transplant experiments at Potterne. Tests with *Ononis* are being continued.

METEOROLOGICAL DATA.

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
1932		°C.	°F.	°C.	°F.	Max. %	Min. %	Week	Month	Week	Month
Jan.	1-7	11.7	53	-2.2	28	88	68	24.50		4	
"	8-14	11.1	52	-2.8	27	88	59	26.75		6	
"	15-21	11.7	53	0	32	89	58	5.00		1	
"	22-28	10.0	50	-1.7	29	90	70	0		0	
"	29-31	8.3	47	-3.3	26	88	57	0	56.25	0	11
Feb.	1-7	8.3	47	-3.9	25	86	56	0		0	
"	8-14	6.7	44	-5.6	22	88	52	0		0	
"	15-21	8.3	47	-5.6	22	90	48	0		0	
"	22-28	10.0	50	-2.2	28	88	33	0		0	
"	29	5.6	42	-2.2	28	87	50	0	0	0	0
Mar.	1-7	11.7	53	-7.2	19	90	36	3.75		3	
"	8-14	13.9	57	-7.2	19	88	37	5.50		1	
"	15-21	13.3	56	-3.9	25	87	37	6.75		1	
"	22-28	14.4	58	0	32	86	29	16.25		3	
"	29-31	13.3	56	2.2	36	84	51	14.25	46.50	3	11
Apr.	1-7	11.7	53	7.8	46	86	36	19.00		5	
"	8-14	13.9	57	-2.8	27	88	37	21.25		5	
"	15-21	12.8	55	0	32	87	40	8.75		6	
"	22-28	15.0	59	0.6	33	88	37	12.25		4	
"	29-30	20.0	68	6.7	44	80	41	7.25	68.50	2	22
May	1-7	13.9	57	-1.1	30	87	35	42.75		5	
"	8-14	20.0	68	0	32	87	28	9.75		3	
"	15-21	22.2	72	7.8	46	84	39	44.75		5	
"	22-28	18.9	66	1.1	34	84	37	16.25		5	
"	29-31	21.7	71	4.4	40	85	40	9.00	122.50	1	19

444 *Transplant Experiments of the British Ecological Society*

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
		°C.	°F.	°C.	°F.	Max. %	Min. %	Week	Month	Week	Month
1932											
June	1-7	25.0	77	1.1	34	84	35	1.25		2	
"	8-14	27.8	82	3.9	39	78	29	0.50		1	
"	15-21	30.6	87	5.0	41	78	24	0		0	
"	22-28	29.4	85	8.9	48	72	26	0.50		1	
"	29-30	23.9	75	13.3	56	64	33	28.00	30.25	2	6
July	1-7	25.6	78	8.3	47	74	34	2.75		2	
"	8-14	31.1	88	10.0	50	67	37	3.25		2	
"	15-21	24.4	76	5.6	42	64	40	6.25		2	
"	22-28	23.3	74	6.7	44	70	28	80.00		7	
"	29-31	23.9	75	12.2	54	62	45	7.75	100.0	3	16
Aug.	1-7	27.8	82	11.1	52	62	34	2.50		2	
"	8-14	33.3	92	10.0	50	80	31	4.75		2	
"	15-21	38.3	101	12.8	55	62	29	13.50		2	
"	22-28	25.6	78	8.9	48	56	36	0		0	
"	29-31	23.9	75	7.8	46	71	29	3.75	24.50	1	7
Sept.	1-7	21.7	71	5.6	42	69	37	30.00		5	
"	8-14	25.6	78	8.3	47	64	38	7.75		3	
"	15-21	25.6	78	5.6	42	64	34	8.50		3	
"	22-28	17.2	63	0.6	33	75	38	26.75		4	
"	29-30	15.6	60	6.7	44	62	55	13.75	86.75	2	17
Oct.	1-7	15.6	60	-1.1	30	69	30	20.75		1	
"	8-14	15.0	59	-0.6	31	71	42	27.50		5	
"	15-21	15.6	60	1.1	34	60	38	36.50		5	
"	22-28	12.2	54	-3.3	26	—	—	34.50		5	
"	29-31	11.7	53	0	32	—	—	5.75	125.00	2	18
Nov.	1-7	13.3	56	-0.6	31	—	—	4.50		2	
"	8-14	11.1	52	-1.1	30	—	—	2.50		3	
"	15-21	7.8	46	-0.6	31	—	—	11.00		3	
"	22-28	11.1	52	0.6	33	—	—	5.00		3	
"	29-30	8.3	47	4.4	40	—	—	10.75	33.75	1	12
Dec.	1-7	8.9	48	-2.2	28	—	—	17.25		3	
"	8-14	10.6	51	-1.7	29	—	—	1.75		2	
"	15-21	12.2	54	3.3	38	—	—	1.25		1	
"	22-28	8.9	48	-1.1	30	—	—	1.75		1	
"	29-31	6.7	44	0	32	—	—	17.25	39.25	2	9
1933											
Jan.	1-7	11.1	52	-1.1	30	—	—	19.75		6	
"	8-14	8.9	48	-5.6	22	—	—	10.75		3	
"	15-21	5.6	42	-5.0	23	—	—	9.50		3	
"	22-28	2.8	37	-9.4	15	—	—	0		0	
"	29-31	10.6	51	0	32	—	—	16.50	56.50	3	15
Feb.	1-7	12.2	54	-1.7	29	—	—	13.50		3	
"	8-14	11.7	53	-5.6	22	—	—	3.75		2	
"	15-21	7.8	46	-8.3	17	—	—	0.75		1	
"	22-28	10.0	50	-6.7	20	—	—	70.50	88.50	4	10
Mar.	1-7	13.9	57	-1.1	30	—	—	22.25		6	
"	8-14	18.9	66	2.8	37	—	—	0.10		1	
"	15-21	13.9	57	-0.6	31	90	42	36.75		6	
"	22-28	22.8	73	-2.2	28	90	22	0		0	
"	29-31	16.1	61	1.7	35	90	48	4.25	63.35	3	16
Apr.	1-7	23.3	74	0	32	93	28	0		0	
"	8-14	21.1	70	-0.6	31	92	27	0		0	
"	15-21	23.3	74	-2.2	28	93	29	0		0	
"	22-28	15.6	60	3.9	39	88	33	26.75		5	
"	29-30	17.8	64	8.3	47	89	43	9.25	36.00	2	7
May	1-7	21.1	70	6.1	43	89	38	16.75		6	
"	8-14	19.4	67	2.8	37	90	33	7.25		4	
"	15-21	30.0	86	6.7	44	87	34	2.00		1	
"	22-28	28.3	83	3.3	38	90	37	14.75		3	
"	29-31	23.3	74	7.8	46	90	44	0.75	41.50	1	15

		Temperature				Relative humidity		Rainfall			
		Max.		Min.		Max.	Min.	Rainfall in mm.		No. of "rain days"	
		°C.	°F.	°C.	°F.			Week	Month	Week	Month
1933											
June	1-7	35.6	96	11.1	52	90	31	0		0	
"	8-14	32.2	90	7.2	45	92	33	2.50		1	
"	15-21	29.4	85	7.8	46	90	38	11.00		3	
"	22-28	31.7	89	8.3	47	90	38	13.00		2	
"	29-30	24.4	76	6.7	44	90	40		26.50	0	6
July	1-7	35.6	96	15.0	59	89	37	0		0	
"	8-14	23.3	74	12.2	54	87	44	52.75		6	
"	15-21	27.8	82	10.0	50	88	43	9.25		3	
"	22-28	34.4	94	10.6	51	91	44	0.75		1	
"	29-31	26.7	80	12.2	54	86	34	1.00	63.75	1	11
Aug.	1-7	33.9	93	15.0	59	88	39	0		0	
"	8-14	29.4	85	13.3	56	88	34	16.50		3	
"	15-21	25.0	77	9.4	49	87	38	3.75		3	
"	22-28	32.2	90	8.3	47	88	39	2.00		1	
"	29-31	27.2	81	6.7	44	87	32	0	22.25	0	7
Sept.	1-7	31.1	88	8.3	47	88	32	0		0	
"	8-14	28.3	83	5.6	42	88	27	25.00		2	
"	15-21	25.0	77	4.4	40	88	36	5.00		5	
"	22-28	21.1	70	5.6	42	86	45	32.25		5	
"	29-30	21.7	71	11.7	53	88	56	1.75	64.00	1	13
Oct.	1-7	22.2	72	4.4	40	88	43	6.75		2	
"	8-14	18.9	66	3.9	39	87	39	14.75		3	
"	15-21	16.7	62	2.2	36	88	45	2.25		1	
"	22-28	13.3	56	-1.1	30	84	39	28.25		4	
"	29-31	13.3	56	2.2	36	86	47	0.50	52.50	1	11
Nov.	1-7	12.2	54	0.6	33	86	52	0.50		1	
"	8-14	12.8	55	-3.3	26	85	50	12.50		3	
"	15-21	15.6	60	-2.8	27	85	58	4.25		2	
"	22-28	9.4	49	-1.1	30	86	50	0		0	
"	29-30	5.6	42	1.1	34	80	64	0	17.25	0	6
Dec.	1-7	5.0	41	-6.7	20	90	56	0		0	
"	8-14	5.0	41	-7.2	19	86	39	1.0		2	
"	15-21	6.1	43	-5.0	23	84	51	0		0	
"	22-28	6.1	43	1.1	34	84	59	9.0		3	
"	29-31	6.7	44	-2.8	27	86	62	1.5	11.5	2	7

The total annual rainfall for 1932 was 733.25 mm. (29.3 in.), and for 1933 the remarkably low value of 543.60 mm. (21.74 in.) was recorded. During the winter of 1932-3 the hygrometer did not function satisfactorily and the relative atmospheric humidity is not given for that period.

BIOTIC FACTORS.

Owing to replanting and consequent surface disturbance in 1932 (*Anthyllis*, *Fragaria*, and *Phleum*) and the dense top-hammer of *Centaurea*, conditions were unsuitable for the appearance of a closed bryophytic vegetation. The drier season of 1933 was also unfavourable to moss growth. In December 1933 bryophytes were most abundant on calcareous sand, least on Potterne soil.

Slug attack became epidemic in 1932 on the clays, especially on *Centaurea*, and steps had to be taken to reduce the population by mechanical picking and the judicious use of powdered alum. Commercial slugicides were purposely avoided in order not to complicate soil analyses. Partly owing to artificial reduction, partly to the drier season, the damage done to plants on the plots by slugs was much less in 1933.

Centaurea nemoralis* Jord. forma *radiata albiflora

Winter condition and deaths. This plant has maintained its growth on all the soils, and the only additional deaths to record are: clay No. 59 (1933), No. 61 (1932), No. 63 (1933); chalky clay No. 90 (1932); reserve No. 145 (1933), No. 147 (1933). None of these has been replaced. In 1932 new growth had commenced by the beginning of March; cold east winds occurred shortly afterwards and the young leaves were so damaged on all the plots that all the unfolded leaves were killed. In the spring of 1933 growth was more forward and had actually commenced in December 1932. It continued without interruption in the spring on all soils. "Top-hamper" again decayed quickest on clay and slowest on calcareous sand. The old withered stems were removed after the fruits were dispersed. This was done to reduce smother and slug attack.

Seedlings.

	Spring, 1932	Spring, 1933	Autumn, 1933
Sand	Numerous	Numerous	Numerous
Calcareous sand	Numerous	Numerous	Numerous
Clay	Very few	Few	Very few
Chalky clay	Numerous	Very few	Very few
Potterne soil	Few	Very few	Very few

The main germination was again in the spring and best on the sands.

General tone. For 1932 and 1933 clay always had the worst tone (five scorings). In 1932 sand had the best tone, in 1933 chalky clay. The final sequence was chalky clay, sand, calcareous sand, Potterne soil, clay. Plants in the central rows again show the damaging effect of smother (see below).

Habit. The marked difference in habit between the plants at Kew (widely ascending stems) and those on all the beds at Potterne (erect stems) was even accentuated.

Stem heights (maximum for each soil).

	15. viii. 32 dm.	7. vi. 33 dm.
Sand	9	9.5
Calcareous sand	9	8.8
Clay	7.8	7
Chalky clay	8.8	9.5
Potterne soil	8.3	8.5

*Numbers of flowering stems per ramet.**

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
Total per soil	1473	1627	1672	1843	806	847	1238	1426	1093	1196
Max. per ramet	100	97	136	127	77	112	100	118	86	114
Min. per ramet	4	14	11	10	2	0	1	5	9	10
Mean per ramet	56.6	62.6	64.2	70.9	35.0	38.5	51.6	59.4	42.0	49.8
Standard deviation	24.6	22.7	33.1	36.1	24.7	26.8	27.7	32.1	21.0	26.4

* A useful term for the individual members of a clone (clon), the latter being the total of separate plants (ramets) produced from an original seedling plant (ortet) by vegetative multiplication and in the absence of somatic mutation (see **Stout, A. B.**, in *J. N. Y. Bot. Gdn.*, **30**, 25, 1919).

The figures in the above table require some explanation and interpretation. All the material belongs to one clone, and, since no somatic mutations have been observed, may therefore, from the genetical standpoint at least, be regarded as one individual. Moreover, *Centaurea nemoralis* does not propagate naturally by vegetative means beyond the close colony stage. It follows that the total number of stems per plot indicates rather more clearly than the other figures the influence of the soil on the species, or rather the variety of the species used, chiefly because in calculating the values for the ramets dead plants (three for clay and two for chalky clay in 1932, and four for clay, two for chalky clay, and two for Potterne soil in 1933) have been omitted entirely. It will be seen that for both years the sequence (largest number of stems first) was calcareous sand, sand, chalky clay, Potterne soil, clay. Again, for every soil there was a larger number of stems produced in 1933 than in 1932, in spite of additional deaths of ramets on clay and Potterne soil. On the other hand, the great ranges between the maximum and minimum number of stems per ramet and absolute and relative values of the standard deviations show the wide range of variation among the ramets on every soil and the increase in this. For every plot the standard deviation was greater in both 1932 and 1933 than it was in 1930 or 1931 (II,¹ p. 273). Again, with the single exception of sand, the standard deviation was greater for 1933 than for 1932. This increased dispersion of the variates (numbers of stems per ramet) is due, probably almost entirely, to the differential effects of competition, especially to shading and smother from "top-hamper" (including its decay). The *Centaurea* ramets on every plot are in four rows, and it is the central plants of the two central rows which show the effect of competition with surrounding ramets. While the outside ramets show luxuriant growth and high numbers of stems, the inside ones show poor growth and few numbers of stems or have even been "stified" out of existence. This phenomenon is shown on all the beds, but most clearly on the clay. One diagram must suffice as an example, that of clay for 1933. In this diagram (Fig. 1) each circle represents one ramet, the upper figure in every circle represents the serial number of the ramet and the lower figure in parentheses the number of flowering stems it had in 1933. While the diagram is not drawn exactly to scale, it shows the relative position of each ramet. Had old "top-hamper" not been removed at all during 1932-3 it is probable that the differences between inner and outer ramets would have been still greater, but then individual ramet scoring for all characters would have been impossible. Root competition may also be involved, but were this an important cause one would expect the right-hand outer row, which is near to the deal boards on one side, to have fewer stems and less luxuriant growth than the left-hand outer row beyond which the soil continues. The mean stems per ramet are:

¹ Throughout this paper, I refers to the first Transplant Report, published in this JOURN. 18, 352 (1930), II refers to the second Transplant Report, published in this JOURN. 21, 268 (1933).

51 to 57 (no deaths)	50.4
59 to 62 (excluding dead ramets)	12.3
59 to 62 (including dead ramets)	9.2
65 to 69 (excluding dead ramets)	17.7
65 to 69 (including dead ramets)	10.6
71 to 74 (no deaths)	38.8

First flowering.

		1932					1933				
		Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil	Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil
June	7	—	—	—	—	—	—	—	8	—	—
"	8	—	—	—	—	—	—	—	10	—	—
"	9	—	—	—	—	—	—	—	13	—	—
"	10	—	—	—	—	—	—	—	14	2	—
"	11	—	—	—	—	—	—	—	16	2	—
"	12	—	—	—	—	—	—	1	16	2	—
"	13	—	—	—	—	—	1	3	20	4	—
"	14	—	—	—	—	—	1	5	—	5	1
"	15	—	—	—	—	—	3	11	—	9	5
"	16	—	—	—	—	—	7	15	—	10	6
"	17	—	—	—	—	—	8	19	—	17	9
"	18	—	—	—	—	—	9	23	—	17	9
"	19	—	—	—	—	—	12	24	—	19	12
"	20	—	—	—	—	—	15	26	—	19	12
"	21	—	—	—	—	—	21	—	—	19	15
"	22	—	—	—	—	—	21	—	—	19	16
"	23	—	—	—	—	—	22	—	—	21	16
"	24	—	—	—	1	—	24	—	—	22	19
"	25	1	1	5	1	—	24	—	—	23	19
"	26	1	2	6	1	—	25	—	—	23	23
"	27	6	6	9	3	2	—	—	—	23	24
"	28	11	13	15	11	6	—	—	—	23	25
"	29	15	15	16	13	8	—	—	—	24	—
"	30	20	21	18	20	10	—	—	—	—	—
July	1	25	26	22	23	17	—	—	—	—	—
"	2	25	—	23	23	18	—	—	—	—	—
"	3	26	—	—	24	22	—	—	—	—	—
"	4	—	—	—	—	23	—	—	—	—	—
"	5	—	—	—	—	25	—	—	—	—	—
"	6	—	—	—	—	26	—	—	—	—	—

Indumentum. This has remained as recorded in the last report. Dr Metcalfe, of Kew, is making an intensive anatomical study of this and other characters of the transplant knapweeds.

Primary flowering. With the removal of old top-hamper it became possible to score individual ramets for the appearance of first flowers (see table). The maximum flowering was during the first week of July (the stock represents an early flowering race), and the order of florifery, the best first, was sand, calcareous sand, Potterne soil, chalky clay, clay.

Completion of primary flowering. The sequence (the first completed placed first) was: 28. vii. 32: calcareous sand, clay, Potterne soil, sand, chalky clay; 10. vii. 33: clay, calcareous sand, chalky clay, sand, Potterne soil.

Secondary flowering was very sparse in 1932 and was completed by

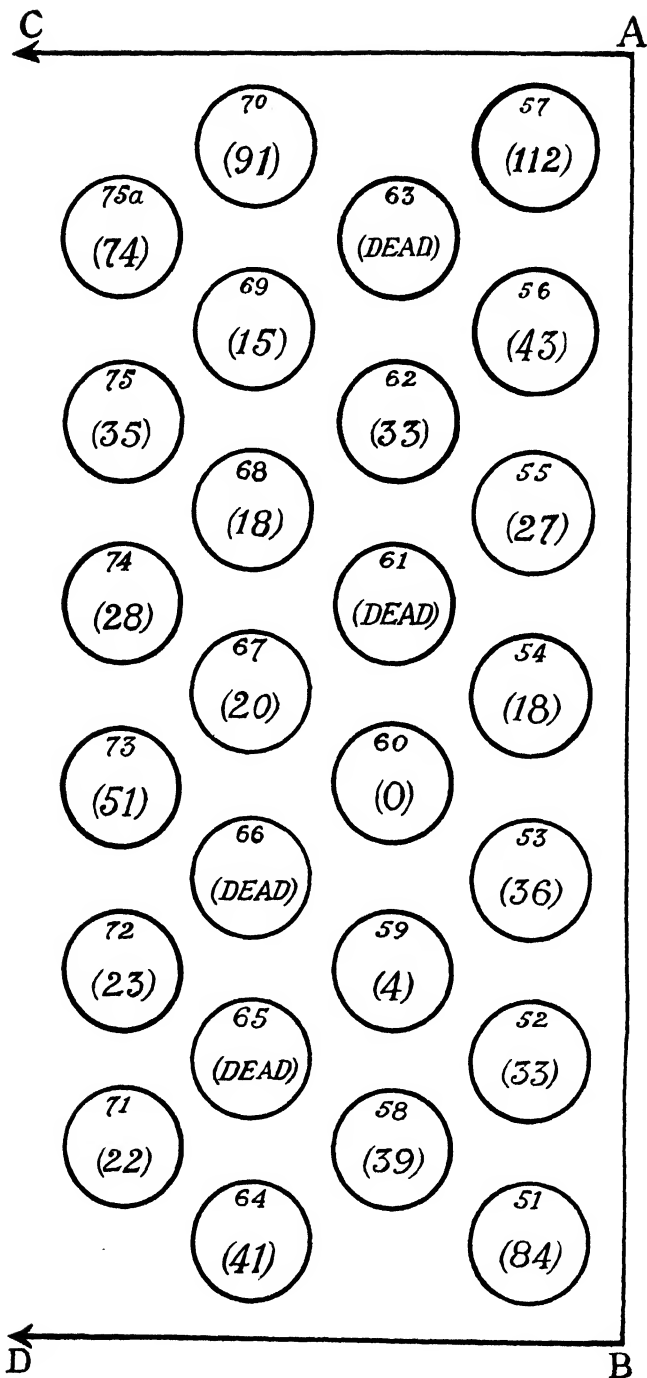


FIG. 1. *Centaurea* plot on clay, 1933; 2-in. deal board on three sides; on the fourth side the soil is continued without a break to the end of the enclosure (35 ft.). From A to B is 10 ft. A to C is 4 ft. 6 in. Numbers in parentheses show numbers of flowering stems on each "ramet" in 1933.

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15. viii. 32; in 1933 it was again sparse except on chalky clay (sand 1, calcareous sand 3, clay 3, chalky clay 15, Potterne soil 1), and was completed by 27. vii. 33.

Silene maritima L.

Winter conditions and deaths. In spite of numerous replacements the plants have died out so that now (December 1933) only eight of the originals and few of the first replacements are alive. It has therefore been thought advisable to recommence with a fresh stock, and clones taken from the original No. 59 (clay) are being recloned. It is hoped that sufficient plants will be available for replanting the beds in 1935. The following table shows the deaths of original plants (not replacements):

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1928-9	5	1	0	0	23
1930-1	13	1	22	25	3
1932-3	1	23	4	1	0
Still alive	7	1	0	0	0

Compared with most of the many other stocks of *S. maritima* grown at Potterne this cannot be considered a hardy or very long-lived one. The plants on Potterne soil grew very luxuriantly the first year and only three survived a move necessitated by rearrangement of the Potterne soil bed. Numerous plants on clay and chalky clay died following a bad attack of slugs and hardening of the surface soil (II, p. 272). Later (8. v. 32) slugs (*Agriolimax agrestis*) spread to the calcareous sand and death of many of the *Silene maritima* plants on this soil followed. Damp, with its resultant increase in attack by slugs, *Phytophthora*, and *Marssonina*, is much more harmful to established *Silene* plants than is drought. No deaths occurred during the period 1932-3 which could be attributed to dryness of the soil, in spite of the small summer rainfall and high soil temperatures of June to September 1933.

Seedlings.

	Spring 9. v. 32	Summer 6. vi. 32	Autumn 20. ix. 32	Spring 11. iv. 33	Summer 7. vi. 33	Summer 11. viii. 33
Sand	Very few	Very few	Numerous	Very few	Few	None
Calcareous sand	None	Very few	Few	Few	Numerous	None
Clay	None	Very few	Numerous	None	Very few	Numerous
Chalky clay	Few	Few	None	None	Very few	None
Potterne soil	Numerous	Very few	None	Very few	Few	Numerous

ROOT SYSTEMS. The decision to discontinue work with the existing stock provided an opportunity to examine the root systems. Those of the living plants that were *in situ* showed marked uniformity of root systems on any one soil. A paper on the anatomy of the roots of *Silene*, as grown on the Transplant soils, but with special reference to *S. vulgaris*, has been published in the *New Phytol.* **33**, 77, 1934.

Sand. The main tap-root was surrounded by about seven large secondaries

branching off 1–3 cm. below the crown and going down, with further branching, straight into the soil. About fourteen more slender secondaries from near the top of the crown spread horizontally for 3–4 cm. and then turned gradually and finally more abruptly into the soil. No tuberous thickenings were seen. The superficial colour of the washed roots was “*Clay Color*” (Ridgway, Plate XXIX).

Calcareous sand. The morphology of the root system was approximately as in sand. The superficial colour of the washed roots was “*Antimony Yellow*” (Ridgway, Plate XV).

Clay. There was no marked main tap-root but about fourteen rather slender secondaries spread vertically from 1–2 cm. below the crown and about fourteen horizontally. The superficial colour of the washed roots was “*Honey Yellow*” (Ridgway, Plate XXX).

Chalky clay. Young seedlings showed a morphology of the root system probably very similar to plants in clay. Ramets had a collar 3–4 cm. long and then a mass of adventitious roots, from a callus area, partly spreading horizontally, partly going down vertically. The superficial colour of the washed roots was “*Chamois*” (Ridgway, Plate XXX).

Potterne soil. About nine slender roots spread horizontally 2–3 cm. below the soil. Below these about eight main root branches coiled round compactly and then extended more or less vertically and branched into the soil. The superficial colour of the washed roots was “*Honey Yellow*” (Ridgway, Plate XXX).

***Anthyllis vulneraria* L.**

The committee decided to continue the experiments with this species, using, however, a smaller number of individuals, twelve on each soil. The seedlings were grown from seeds of original plants selfed in 1929, under cages, *in situ* on the respective soils. The seeds were sown on March 24th, 1932, in soils similar to those into which they were later transplanted. Germination (in heat) was uniformly excellent. They were finally transplanted on July 1st, 1932.

Deaths in 1932: i.e. before flowering (recorded up to October 1932, up to about 7 months old). Sand, No. 9; calcareous sand, No. 34; Potterne soil, Nos. 126, 128, 133, 135.

All dead plants were replaced by plants of the same age which had been growing an equal time on the same soils. No more deaths had occurred up to April 11th, 1933, and all plants flowered.

Tone of seedlings (vigour, growth, and general health, placing the best first).

14. iv. 32	11. vii. 32	27. xii. 32	11. iv. 33
Potterne soil	Potterne soil	Potterne soil	Calcareous sand
Sand	Clay	Clay	Clay
Clay	Sand	Calcareous sand	Sand
Calcareous sand	Calcareous sand	Sand	Chalky clay
Chalky clay	Chalky clay	Chalky clay	Potterne soil

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Number of stems per plant.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Maximum	56	78	62	44	91
Minimum	16	16	36	17	27
Mean	44.2	58.5	52.7	37.6	62.8

Stem heights in decimetres (recorded 22. vi. 33).

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Maximum	7 (No. 1)	6.25 (No. 29)	5.5 (No. 61)	6.75 (No. 86)	6 (No. 136)
Minimum	5.25 (No. 9)	4.25 (No. 28)	4.5 (No. 56)	5.5 (No. 82)	5 (No. 126)

The number of flower heads was up to 6 per stem (mostly 5) for sand; up to 7 (mostly 5) for calcareous sand; up to 5 (mostly 4) for clay; up to 6 (mostly 5) for chalky clay; up to 6 (mostly 6) for Potterne soil.

Number of flowers per head.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Means	21.8	20.2	21.6	21.3	20.73

These means are so close that there are probably no real significant differences due to the soil in this character. A general survey of the counts confirms this.

First flowering, 1933.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
May 3	—	2	—	—	—
" 4	2	2	3	—	1
" 5	2	4	3	—	2
" 6	2	7	6	—	4
" 7	5	9	7	—	6
" 8	5	11	9	—	6
" 9	6	11	10	1	7
" 10	7	11	12	2	10
" 11	9	12	—	2	11
" 12	12	—	—	5	12
" 13	—	—	—	7	—
" 14	—	—	—	10	—
" 15	—	—	—	12	—

Florifery. The plants were in full flower during the first week of June 1933, and the order, most floriferous first, was: calcareous sand, clay, Potterne soil, sand, chalky clay. The general tone of the plants at this time was in the same sequence.

Summer deaths (at or after primary flowering): sand, Nos. 1, 2, 3, 4, 6, 12; calcareous sand, No. 27; clay, Nos. 56, 58; chalky clay, No. 77; Potterne soil, Nos. 128, 137.

Secondary flowering from lateral shoots July 10th, 1933. All living plants except one on clay and one on Potterne soil showed secondary flowering. Tone at this date was chalky clay (best), calcareous sand, Potterne soil, clay, sand.

Autumn deaths. All plants were dead by 11. xii. 33 except one on calcareous sand, two on clay, six on chalky clay, five on Potterne soil.

Plasticity. No morphological changes were recorded on any of the soils. The plants retained their specific and varietal characters with remarkable constancy. Even the small amount of colour in the calyx reappeared in all plants.

Cause of deaths. It was suspected that the luxuriant growth of plants in cultivation, partly connected with the absence of competition with other vegetation and of grazing by rabbits and sheep, might account for the relatively high death rate at or shortly after flowering. The lush growth of the cultivated plants appears to make them more susceptible to attacks by root and crown attacking fungi (*Verticillium*).

The following tables, obtained by the analysis of random samples from two wild populations, compared with the figures given in this and previous reports, indicate clearly that plants in the wild make much less growth and produce fewer flowering stems, flower-heads per stem, and flowers per head, than those grown as Transplants at Potterne. It should be noted that one of the samples is of the population from which the parent of the Transplant stock was originally obtained.

All Canning's Down, Wiltshire, 15. vi. 1933. Twelve plants.

Mean number of stems per plant	Mean length of stems	Mean number of heads per plant	Mean number of flowers per head
6.6	2.55 dm.	2.6	11.8

The biotic factor of grazing sheep was important here.

Harbury, Warwickshire, 2. vii. 1933. Sixteen plants.

Mean number of stems per plant	Mean length of stems	Mean number of heads per plant	Mean number of flowers per head
6.1	2.58 dm.	2.4	10.1

Of the total number of seventy-three stems in the Harbury sample, twenty-three were eaten off; usually these were the taller stems. In both populations plants which had been browsed generally showed an increased number of stems due to tillering.

Seedlings. Seeds from the two generations dealt with in previous reports fell into the ground and the following records refer to germination of seed which has been in the soil four or fewer years.

	6. iv. 32	8. v. 32	11. vii. 32	20. ix. 32	4. iv. 33	7. vi. 33	23. vii. 33	11. viii. 33	11. xii. 33
Sand	Numerous	Numerous	Numerous	None	Very few	Many	Few	Few	Very numerous
Calcareous sand	Numerous	Very numerous	Numerous	None	Few	Very numerous	Few	Many	Very numerous
Clay	Many	Numerous	Numerous	None	None	Few	Few	Few	Numerous
Chalky clay	Many	Numerous	Numerous	None	Few	Very numerous	Few	Few	Numerous
Potterne soil	Few	Numerous	Numerous	None	Very few	None	Few	Many	Numerous

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The seedlings recorded in the last two columns were from new seed which germinated immediately after falling.

Seeds, collected in 1929, had their germination tested (in the Hearson germinator at the Chelsea College of Science in February 1932), with the following results:

Sand	18	germinated out of 20
Calcareous sand	20	„ 20
Clay	12	„ 20
Chalky clay	13	„ 20
Potterne soil	14	„ 20

Germination must have been very quick because the seeds were only placed in the germinator on porcelain dishes on February 4th and by February 10th some of the seedlings were 16 mm. long and had green cotyledons expanded.

Chromosome number. A short time before his death the late Mr L. H. Stone, of the John Innes Horticultural Institution, informed us that the Transplant *Anthyllis* stock had twelve somatic chromosomes as counted in root-tips. One pair was much larger than the others. The twelve chromosomes probably pair up but the smaller ones are all very similar.

***Plantago major* L.**

Deaths. The following table indicates the deaths which have taken place amongst the original plants since the beginning of the experiments:

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1928-9	15	0	0	0	15
1930-1	5	19	0	20	6
1932-3	4	3	1	0	1
Still alive	1	3	24	5	3

Drought and frost lifting appear to be the main immediate causes of death on the sands, correlated with the development of a shallow root system. An attack of *Ramularia plantagineae* accentuated by slugs weakened the plants on the chalky clay and many of them died in the autumn of the same year. An attack of wireworm on the Potterne soil, virgin soil from under old turf, caused the deaths of fifteen plants early in their history.

Most of the dead plants have been replaced, some several times, by seedlings grown on the same soil type and derived from seed obtained by sowing a plant *in situ* under control.

Diseases. *Ramularia* attacks did little serious damage in the period 1932-3 but the fungus was evident on chalky clay and Potterne soil.

Winter condition. Sands. Only one crown is usually produced by a plant, but up to four may develop.

Clays. The central crowns die, rot, and are pushed out by the growth of the inner leaves of three to fifteen lateral rosettes which extend the plant in all directions. No single crowns now occur.

Potterne soil. The growth is mostly similar to that on the clays, with one to eight crowns.

There is a tendency for plants on the clays to lose some of their lateral rosettes with increased age, and to reduce the production of new ones. By December 27th, 1932, young growth had started on all plants. On Potterne soil old leaves were retained, while on the other soils most of the old leaves had been shed. By April 1933 all plants had lost all their old leaves. There is complete die back in the winter, even in a mild season.

Habit. The fluctuations between strict and flat habit are best expressed in a table as follows; the plants not counted having only flat rosettes:

	9. v. 32		6. vi. 32		11. vii. 32		15. viii. 32		20. ix. 32		11. iv. 33		16. vi. 33	
	Strict	Inter-med.	Strict	Inter-med.	Strict	Inter-med.	Strict	Inter-med.	Strict	Inter-med.	Strict	Inter-med.	Strict	Inter-med.
Sand	0	3	3	0	0	0	0	1	0	4	0	0	1	0
Calcareous sand	6	2	0	10	0	2	3	0	2	0	2	6	1	0
Clay	0	0	0	2	0	2 ^b	1	18 ^c	2	17 ^c	0	1 ^b	0	10 ^c
Chalky clay	11 ^a	0	11 ^a	0	3 ^a	0	10 ^a	0	2 ^d	5	6	0	1	7 ^f
Potterne soil	0	1	0	1	0	1 ^b	1	0	6	0	1	5 ^b	1	11 ^g

^a One plant had one rosette flat.

^b Every plant with one rosette strict, the remainder flat.

^c Perhaps due to mechanical bunching up of the crowns rather than to an intermediate development of "strictness".

^d Two rosettes of one plant strict.

^e Four plants with one and one with three strict rosettes.

^f Including one plant with three strict and two flat rosettes.

^g Including two plants each with one, and one plant with two, strict rosettes.

At present no explanation of the peculiar fluctuation of one and the same plant, or even one rosette of a plant, between the strict and flat habit is forthcoming. The extreme conditions are so strikingly different that they could not be ignored. There seems at present to be no significant correlation between the fluctuations and soil, age, and season.

Seedlings.

	9. v. 32	15. viii. 32	20. ix. 32	11. iv. 33	7. vi. 33	10. vii. 33
Sand	Numerous	Numerous	None	Numerous	Very numerous	Many
Calcareous sand	Very few	Very few	Few	Very few	Very numerous	Many
Clay	Very few	Very few	Very few	Few	Numerous	Few
Chalky clay	None	Few	Very few	None	Very few	Few
Potterne soil	Numerous	Few	Numerous	Very numerous	Very numerous	Very few

Old infructescences persist on the plant till the year following their seed setting. Germination is, on the whole, continuous throughout the spring, summer, and autumn, and seed may remain dormant in the soil at least till the year after its formation.

General tone (best first).

6. vi. 32, 11. vii. 32

Potterne soil
Clay
Sand
Calcareous sand
Chalky clay

15. viii. 32

Potterne soil
Clay
Sand
Chalky clay
Calcareous sand

7. vi. 33, 11. xii. 33

Potterne soil
Clay
Chalky clay
Calcareous sand
Sand

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Indumentum. On the sands the hairs on the flowering peduncles are spreading (or subspreading) at least in the lower part. On the clay the peduncles have adpressed hairs above and are glabrous or glabrescent in the lower part. On chalky clay the peduncles generally have few hairs which may be either spreading or adpressed. On Potterne soil the hairs are few, adpressed above, spreading in the centre, and absent below.

Diameters or heights of rosettes in cm. (diameters refer to flat rosettes, heights to strict or semi-strict ones).

	Flat rosette diam.				Strict or semi-strict rosette height			
	Max.	Plant No.	Min.	Plant No.	Max.	Plant No.	Min.	Plant No.
August 15th, 1932								
Sand	15	10	8	1	3.5	15	—	—
Calcareous sand	9	27	—	—	13	29	—	—
Clay	43	60	14.5	69	—	—	—	—
Chalky clay	12.5	78	—	—	10	78	4.5	77
Potterne soil	38	146	19.5	127	20.5	148	—	—
June 7th, 1933								
Sand	16	25	4.3	11	—	—	—	—
Calcareous sand	12.3	49	4.7	36	5.5	34	3.2	31
Clay	39	60	18.3	53	12.2	74	10	53
Chalky clay	20.1	95	10.6	87	8	83	4	91
Potterne soil	43.5	145	22	126	20.5	143	10.5	148

Length of infructescences.

Soil	Plant No.	Spike and peduncle dm.	Spike alone dm.
August 15th, 1932.			
Sand	Max.	10	1.5
	Min.	6	0.35
Calcareous sand	Max.	29	2
	Min.	27	0.6
Clay	Max.	60	3.0
	Min.	169	1.35
Chalky clay	Max.	78	2.12
	Min.	77	0.75
Potterne soil	Max.	148	3.0
	Min.	127	2.2
August 11th, 1933.			
Sand	Max.	25	1.7
	Min.	6	0.27
Calcareous sand	Max.	49	1.55
	Min.	26	0.35
Clay	Max.	60	2.27
	Min.	52	1.6
Chalky clay	Max.	83	1.8
	Min.	77	0.71
Potterne soil	Max.	143	3.25
	Min.	142	1.41

For the minima the longest infructescence on the plant with the shortest fully developed infructescence was measured. There was a general tendency for "strict" plants to have longer infructescences than "flat" plants. This tendency was even obvious in "strict" and "flat" rosettes of the same plant.

Thus in No. 78 the maximum spike + peduncle for a "flat" rosette was 0.9 dm., spike 0.6 cm., while for a strict rosette the corresponding figures were 2.12 dm., and 1.2 dm.

Spikes per plant.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
Maximum	30	18	24	14	156	173	29	35	82	69
Minimum	1	2	2	2	29	16	7	3	30	10
Mean	12.2	7.4	8.5	6.8	68.0	66.6	14.7	12.2	55.6	46.1
Standard deviation	6.8	4.3	6.5	3.6	28.2	33.2	7.7	7.7	13.2	15.9

Primary flowering. Numbers of plants in flower.

		1932					1933				
		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
June	3	—	—	—	—	—	3	2	—	—	—
"	4	—	—	—	—	—	3	2	3	—	4
"	5	—	—	—	—	—	3	2	4	—	5
"	6	—	—	—	—	—	3	2	6	—	8
"	7	—	—	—	—	—	3	2	8	—	11
"	8	—	—	—	—	—	3	2	10	1	14
"	9	—	—	—	—	—	3	2	13	1	15
"	10	—	—	—	—	—	3	2	14	2	16
"	11	—	—	2	—	—	3	2	16	2	16
"	12	—	—	4	1	1	3	2	19	3	18
"	13	—	—	5	1	1	4	4	20	6	21
"	14	—	—	5	1	3	4	4	23	6	22
"	15	—	—	5	1	5	4	6	23	7	22
"	16	—	—	7	1	6	4	7	23	7	22
"	17	2	—	14	1	13	4	7	23	8	23
"	18	4	—	18	1	17	4	8	24	12	23
"	19	5	—	23	2	22	4	8	24	15	23
"	20	5	2	25	2	23	6	8	25	15	23
"	21	5	2	—	2	24	6	8	—	16	24
"	22	5	2	—	2	24	9	8	—	18	24
"	23	5	2	—	4	24	10	8	—	18	25
"	24	5	2	—	4	24	10	10	—	23	—
"	25	8	3	—	4	24	11	12	—	23	—
"	26	8	3	—	5	24	11	12	—	24	—
"	27	10	3	—	6	25	14	15	—	24	—
"	28	10	3	—	7	—	14	17	—	24	—
"	29	11	4	—	8	—	14	17	—	24	—
"	30	12	4	—	8	—	15	19	—	25	—
July	1	15	4	—	8	—	15	20	—	—	—
"	2	16	4	—	8	—	15	20	—	—	—
"	3	16	4	—	8	—	15	20	—	—	—
"	4	17	6	—	8	—	18	22	—	—	—
"	5	18	6	—	9	—	18	22	—	—	—
"	6	19	6	—	9	—	19	22	—	—	—
"	7	20	6	—	9	—	19	22	—	—	—
"	8	20	6	—	9	—	20	22	—	—	—
"	9	20	6	—	10	—	20	22	—	—	—
"	10	21	6	—	10	—	20	22	—	—	—
"	11	22	7	—	10	—	20	22	—	—	—
"	12	22	7	—	10	—	20	22	—	—	—
"	13	22	7	—	10	—	21	22	—	—	—
"	14	22	7	—	10	—	21	24	—	—	—
"	15	23	7	—	10	—	22	24	—	—	—
"	16	23	7	—	10	—	22	24	—	—	—
"	17	23	7	—	10	—	22	24	—	—	—

1932						1933							
		Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil			Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil
July	18	23	8	—	10	—	23	25	—	—	—	—	—
"	19	24	8	—	10	—	—	—	—	—	—	—	—
"	20	—	8	—	10	—	—	—	—	—	—	—	—
"	21	—	8	—	10	—	—	—	—	—	—	—	—
"	22	—	8	—	11	—	—	—	—	—	—	—	—
"	23	—	8	—	12	—	—	—	—	—	—	—	—
"	24	—	8	—	—	—	—	—	—	—	—	—	—
"	25	—	9	—	—	—	—	—	—	—	—	—	—
"	26	—	9	—	—	—	—	—	—	—	—	—	—
"	27	—	9	—	—	—	—	—	—	—	—	—	—
"	28	—	9	—	—	—	—	—	—	—	—	—	—
"	29	—	9	—	—	—	—	—	—	—	—	—	—
"	30	—	10	—	—	—	—	—	—	—	—	—	—

Including the above table, flowering records for 4 years have now been published for *Plantago major*. They show a remarkable general uniformity. The earlier flowering and more rapid completion of the first flowering records on the clays was maintained and on Potterne soil the plants (recorded here for the first time) obviously behave as on the clays. Plants on calcareous clay in 1932 had suffered very severely from *Ramularia* and slug attack, and owing to weakening of the plants not killed the flowering was retarded. The 1933 scoring was again normal.

***Fragaria vesca* L.**

Origin. From south and east aspects of a hill about 170 m. altitude near Hascombe Place, Godalming, Surrey, April 28th, 1930, comm. C. T. Musgrave.

Description (of plant as received from the wild). A small plant up to 9 cm. from soil level to top of flowering stem. *Runners* slender, with internodes up to 16 cm. long, at first densely covered with adpressed white silky hairs, with age the hairs become fewer per cm. and finally become subspreading. *Flowering stem* terete, slender, with adpressed hairs in the upper part and long subspreading hairs below. *Leaves* up to eight per rosette, trifoliate, leaflets elliptic in general shape, apex rounded (apart from the teeth), central leaflet cuneate from just below the middle and in lower part without teeth, the lateral leaflets asymmetrically cuneate, average 2 cm. long, 1.6 cm. broad, terminal leaflet sharply toothed from just below the middle upwards, lateral leaflets with teeth much lower on the outer than on the inner margin, long silky adpressed hairs mainly on the veins on the lower surface, scattered on the upper surface and less strongly adpressed; petiole averaging 2.3 cm. long, with dense silky spreading whitish grey hairs; stipules lanceolate acute or shortly acuminate, 7–12 mm. long, with dense adpressed grey hairs on the back down the midrib, glabrous on the inside. *Inflorescence* three to five-flowered. *Episepals* elliptic-lanceolate, acute, entire at margin, toothed or even two-lobed at apex, 4 mm. long, 1.75 mm. broad, hairy on both surfaces. *Sepals* ovate with a long acumen, 7 mm. long, 2.75 mm. broad, hairy on both

surfaces. *Petals* oblate-rounded, rounded-truncate at the apex, shortly and broadly cuneate at base, about 7 mm. long and 7 mm. broad, white. *Stamens* glabrous, with filaments up to 1.5 mm. long, anthers 0.75–1 mm. long. *Carpels* 0.6–0.8 mm. long, glabrous. *Fruits* broadly ovoid, up to 6 mm. long and 5 mm. in diameter.

The fifty-two plants (in part ramets) received from the wild were grown at Potterne. Forty-nine were scored as phenotypically uniform into one group and three into a second group. It was from one plant of the larger group that the whole of the Transplant stock was raised by a double cloning on August 9th, 1930 and August 17th, 1931. The ramets were planted out into the beds on March 28th, 1932, as single rosettes.

Deaths.

1932 (September): Sand, No. 25A.

1933 (up to July): Sand, No. 8; Calcareous sand, No. 49.

General tone. In May 1932 all plants had established themselves and showed equally good tone. On June 6th the plants on Potterne soil showed most vigorous growth, and it was impossible to differentiate between those on the other soils. Later records are tabulated, the best first, as follows:

11. vii. 32	15. viii. 32
Potterne soil	Potterne soil
Clay	Clay
Sand	Sand
Chalky clay	Calcareous sand
Calcareous sand	Chalky clay

Later records (for 20. ix. 32, 27. xii. 32, 11. iv. 33, 11. vii. 33, 11. xii. 33) gave exactly the same sequence as for 15. viii. 32. The sequence for the number of leaves remaining green on the plants in winter (27. xii. 32, and 12. xii. 32) was also the same. Several plants, occupying a semicircle near the centre of the bed on Potterne soil, appeared to have something affecting their root system during 1933.

Heights of fruiting stems in cm., July 10th, 1933.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Maximum	30.0	26.5	33.0	23.0	42.5
Minimum	9.0	7.0	15.0	6.5	15.5
Mean	19.8	16.1	26.0	14.2	30.0
Standard deviation	5.2	4.3	4.7	3.6	7.9

Runners. These were removed and counted periodically (seven times in 1932, five times in 1933) except that on every soil four plants (at the edge of the beds) were allowed to runner freely and their runners were not included in preparing the following table. It was noted that plants from which runners were removed developed new runners which were stouter than those of plants from which runners were not removed. The parent plants are, for every soil, on the whole larger and with more leaves when the runners are regularly removed than when they are not. This difference was least noticeable

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on the calcareous sand. On Potterne soil the parent plants from which the runners were not removed became unrecognisable in the mass of runner rosettes.

Number of runners produced per year.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil		Kew	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
Total per plot	603	553	332	489	853	2166	241	238	1349	3410	1000	2088
Maximum per ramet	52	65	26	49	56	182	17	23	126	359	64	172
Minimum per ramet	15	4	3	3	21	44	5	2	8	26	15	9
Mean per ramet	27.4	26.3	15.1	23.3	38.8	98.5	10.9	10.6	61.3	155.0	37.0	77.3
Standard deviation	9.9	15.5	5.0	11.5	11.6	35.5	3.2	5.1	30.2	90.3	12.2	35.2

One Kew plant died during the winter 1932-3 but was not replaced and is counted in the analysis for 1933 as producing no runners.

For maximum and mean heights of flowering stems, and for maximum and mean numbers of runners the sequence, tallest or most first, is: Potterne soil, clay, sand, calcareous sand, and chalky clay. For numbers of runners the standard deviation has considerably increased for every soil as between 1932 and 1933. The very large standard deviation for Potterne soil for 1933 is noteworthy.

First flowering.

	1932					1933				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
April 28	—	—	—	—	—	6	7	1	6	2
" 29	—	—	—	—	—	7	8	2	8	4
" 30	—	—	—	—	—	7	8	3	11	4
May 1	—	—	—	—	—	7	9	3	11	4
" 2	—	—	—	—	—	8	10	9	12	6
" 3	—	—	—	—	—	8	10	9	13	6
" 4	—	—	—	—	—	12	12	14	13	13
" 5	—	—	—	—	—	13	15	15	19	17
" 6	—	—	—	—	—	15	17	17	20	19
" 7	—	—	—	—	—	15	18	20	21	19
" 8	—	—	—	—	—	15	18	21	22	21
" 9	—	—	—	—	—	16	18	22	23	21
" 10	—	—	—	—	—	17	19	22	24	21
" 11	—	—	—	—	—	20	21	22	24	24
" 12	—	—	—	—	—	21	22	22	24	25
" 13	—	—	—	—	—	22	22	23	24	25
" 14	—	—	—	—	—	22	24	24	24	26
" 15	—	—	—	—	—	23	26	24	26	—
" 16	1	—	1	2	1	25	—	25	—	—
" 17	1	—	1	2	1	—	—	25	—	—
" 18	2	—	1	2	1	—	—	26	—	—
" 19	2	—	1	2	1	—	—	—	—	—
" 20	2	—	1	2	1	—	—	—	—	—
" 21	5	7	6	4	7	—	—	—	—	—
" 22	9	12	7	7	11	—	—	—	—	—
" 23	10	17	9	8	13	—	—	—	—	—
" 24	12	17	10	9	13	—	—	—	—	—
" 25	14	20	12	9	15	—	—	—	—	—
" 26	15	20	12	13	18	—	—	—	—	—
" 27	15	22	13	14	20	—	—	—	—	—
" 28	17	22	15	16	21	—	—	—	—	—
" 29	21	25	20	19	24	—	—	—	—	—
" 30	24	25	22	21	25	—	—	—	—	—
" 31	25	26	23	22	25	—	—	—	—	—
June 1	25	—	24	23	25	—	—	—	—	—
" 2	25	—	24	23	25	—	—	—	—	—

		1932					1933				
		Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil	Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil
June	3	26	—	24	25	25	—	—	—	—	—
"	4	—	—	25	25	25	—	—	—	—	—
"	5	—	—	25	25	26	—	—	—	—	—
"	6	—	—	25	26	—	—	—	—	—	—
"	7	—	—	25	—	—	—	—	—	—	—
"	8	—	—	25	—	—	—	—	—	—	—
"	9	—	—	26	—	—	—	—	—	—	—

First fruiting.

June	6	—	—	—	—	—	—	1	—	—	—
"	7	—	—	—	—	—	—	1	—	—	—
"	8	—	—	—	—	—	—	1	—	—	—
"	9	—	—	—	—	—	—	1	—	—	—
"	10	—	—	—	—	—	—	2	—	2	3
"	11	—	—	—	—	—	1	2	—	2	6
"	12	—	—	—	—	—	9	4	2	5	16
"	13	—	—	—	—	—	15	9	10	15	22
"	14	—	—	—	—	—	21	15	18	18	23
"	15	—	—	—	—	—	22	18	26	21	26
"	16	—	—	—	—	—	24	23	—	24	—
"	17	—	—	—	—	—	25	25	—	26	—
"	28	—	—	—	—	3	—	—	—	—	—
"	29	—	1	1	1	4	—	—	—	—	—
"	30	—	2	1	1	5	—	—	—	—	—
July	1	—	3	2	1	9	—	—	—	—	—
"	2	2	7	2	1	11	—	—	—	—	—
"	3	4	9	2	3	13	—	—	—	—	—
"	4	6	9	2	4	17	—	—	—	—	—
"	5	6	9	2	4	20	—	—	—	—	—
"	6	6	10	2	6	23	—	—	—	—	—
"	7	9	10	2	8	24	—	—	—	—	—
"	8	9	13	5	13	26	—	—	—	—	—
"	9	11	13	9	19	—	—	—	—	—	—
"	10	19	19	23	24	—	—	—	—	—	—
"	11	23	20	25	25	—	—	—	—	—	—
"	12	24	22	26	26	—	—	—	—	—	—
"	13	24	25	—	—	—	—	—	—	—	—
"	14	24	25	—	—	—	—	—	—	—	—
"	15	26	26	—	—	—	—	—	—	—	—
"	16	—	—	—	—	—	—	—	—	—	—

In the tables for first flowering and first fruiting the date was recorded on which a plant had its first flower fully expanded or its first fruit fully coloured respectively. There appears to be no significant differences between the plants on the different soils in these characters for 1932 and 1933. On the other hand, both tables indicate a very marked difference between 1932 and 1933, the latter year on all soils having earlier flowers and fruits. For fruits there is an actual gap of 10 clear days between first ripening in 1932 and first ripening in 1933. Whether this was due to a year's longer establishment, or to the warmer period preceding and during flowering, must remain undecided till data for several more years are available.

Florifery and fructifery. The sequence (most floriferous and fructiferous first) was:

1932: Potterne soil, clay, chalky clay, sand, calcareous sand.

1933: Potterne soil, clay, sand, calcareous sand, chalky clay.

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In 1933 the fruit size was recorded (largest first) as: Potterne soil, clay, chalky clay, sand, calcareous sand.

Data for statistical analysis were not collected, but the following measurements are for fruits selected as representative of those on the respective soils:

Sand	1.1 cm. long,	1.1 cm. diam.
Calcareous sand	0.9	0.8
Clay	1.2	1.1
Chalky clay	0.8	0.8
Potterne soil	1.4	1.3

1932 runners flowered and fruited in 1933 (on four plants on every soil) in the following order (best first): Potterne soil, clay, sand, calcareous sand, chalky clay.

Secondary flowers were recorded (13. vii. 33) for plants on sand 7, calcareous sand 1, clay 12, chalky clay 2, Potterne soil 17.

Seedlings.

	20. ix. 32	11. iv. 33	7. vi. 33	10. vii. 33	12. xii. 33
Sand	Few	None	None	Very few	Many
Calcareous sand	Very few	None	None	Very few	None
Clay	Numerous	None	Very few	Very few	Numerous
Chalky clay	Very few	None	Very few	Very few	Very few
Potterne soil	Few	None	Many	Many	Many

There is immediate and also delayed germination, and germination may also be continuous through summer and autumn. On clay, in September 1932, seeds actually germinated while fruits were still attached to the parent plant.

Phleum pratense.

The committee decided to use two "types"¹ of *Phleum pratense* kindly provided by Dr J. W. Gregor of the Scottish Plant Breeding Station, Corstorphine, Edinburgh. Dr Gregor has dealt with the genetics and cytology (in co-operation with Dr F. W. Sansome) of *Phleum*, in several publications, notably in *J. Genet.* **17**, 359, 1927, *J. Genet.* **22**, 373, 1930, and *New Phytol.* **30**, 207, 1931.

Dr Gregor has furnished us with the following particulars:

Cb 99 (1) referred to hereafter as "diploid".

Cb 94 (25) referred to hereafter as "hexaploid".

"Cb 99 (1) represents a type which is generally distributed over Britain, but has a decided preference for rather dry soils, whereas Cb 94 (25) is typical of the moist meadow timothy of cultivation. Another ecological factor which apparently influences the distribution of the two types is the grazing animal. In general the diploid form thrives in the presence or absence of grazing, while the hexaploid has a decided preference for the ungrazed habitat.

¹ In this report these are referred to as *P. pratense diploid* and *P. pratense hexaploid* as identified by Dr Gregor. We have not investigated their taxonomic status.

Habitat conditions:

Plant Cb 99 (1) (*diploid*) collected from a sub-upland habitat (600 ft. above sea level) in East Lothian. Grazed by sheep. Geological formation—Old Red Sandstone. A light dry soil. Average annual rainfall 22 inches. A somewhat similar diploid form is found occupying a limestone habitat within $1\frac{1}{2}$ miles of the above-mentioned habitat.

Plant Cb 94 (25) (*hexaploid*) collected from a lowland meadow in Stirlingshire. Ungrazed. Geological formation—Recent. A moist clay soil in the Carse of Stirling.

I believe that within the *P. pratense-alpinum* group there is a graded series with regard to moisture requirements from the very dry to the very moist habitat as follows: $2n$ *P. pratense* (dry), $6n$ *P. pratense* (moist), and $4n$ *P. alpinum* (wet).

Since it is possible that the hexaploid *P. pratense* is the result of diploid *P. pratense* \times tetraploid *P. alpinum* the two extremes, i.e. $2n$ *P. pratense* and $4n$ *P. alpinum*, would probably give the best results from your point of view, but I purposely did not suggest the latter for a first trial as unfortunately it is rather difficult to cultivate even at Edinburgh. However, should the plants Cb 99 (1), and Cb 94 (25) yield satisfactory results it might be worth while trying out *P. alpinum*, the triploid hybrid ($2n$ *P. pratense* \times $4n$ *P. alpinum*) and the pentaploid hybrid ($6n$ *P. pratense* \times $4n$ *P. alpinum*)."

Phleum pratense—diploid.

No deaths have so far occurred.

General tone. On 6. vi. 32 the plots were recorded in the sequence (best first): Potterne soil, clay, sand, chalky clay, calcareous sand. By 15. viii. 32 the sequence was: Potterne soil, clay, chalky clay, sand, calcareous sand, and this sequence was maintained through the remaining months of 1932 and throughout 1933. The summer drought of 1933 killed off most of the basal leaves.

Diameter of plants, 7. vi. 33.

	Max. (dm.)	Min. (dm.)
Sand	3.6 (No. 7)	2.9 (No. 9)
Calcareous sand	3.8 (No. 39)	2.9 (No. 48)
Clay	5.8 (No. 75)	4.7 (No. 75 A)
Chalky clay	4.1 (No. 99)	3.6 (No. 95)
Potterne soil	6.8 (No. 146)	5.2 (No. 143)

Number of stems, stem heights and spike lengths.

The following tables give the results of analyses made on material harvested, after flowering, but before the fruits had fallen, in 1932 and 1933.

Number of stems per ramet.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
Maximum	68	196	67	147	123	510	89	250	230	662
Minimum	28	92	22	66	27	169	29	100	91	343
Mean	47.5	137.9	40.4	108.8	57	301	55.9	164.7	168.3	486.2
Standard deviation	10.5	29.7	10.5	22.6	26.5	89.4	16.1	42.4	32.6	77

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Longest stem length per ramet in cm.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
Maximum	58	45	62	47	53	60	59	67	64	67
Minimum	50	30	44	32	40	50	43	30	48	47
Mean	52.6	36.6	54	39.5	44.8	54.2	50	41	57.7	59.1
Standard deviation	2.2	4.3	3.8	3.5	3.5	2.5	4.5	8.3	3.5	4.7

Shortest stem length per ramet in cm.

	Sand 1932	Calcareous sand 1932	Clay 1932	Chalky clay 1932	Potterne soil 1932
Maximum	25	29	24	25	29
Minimum	12	11	13	11	11
Mean	18.2	18.6	19.5	17.7	21
Standard deviation	3.6	4.3	3.2	3.4	4.3

Maximum spike length per ramet in cm.

	Sand 1933	Calcareous sand 1933	Clay 1933	Chalky clay 1933	Potterne soil 1933
Maximum	12	15	20	15	20
Minimum	7	10	12	10	15
Mean	9.6	11.3	15.8	11.6	17.5
Standard deviation	1.8	1.6	2.6	1.7	2.2

First flowering.

1932						1933				
	Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil	Sand	Cal- careous sand	Clay	Chalky clay	Pot- terne soil
July 15	1	—	—	—	1	1	—	17	2	10
" 16	1	—	1	—	1	1	—	17	2	10
" 17	7	4	10	4	22	2	4	23	6	15
" 18	8	4	10	4	22	2	4	23	6	15
" 19	9	5	10	4	22	6	8	26	9	21
" 20	19	19	17	10	24	6	10	—	11	21
" 21	21	20	18	10	25	10	11	—	16	22
" 22	21	20	18	10	25	16	15	—	17	24
" 23	21	20	18	10	25	18	20	—	22	25
" 24	23	23	20	17	25	22	23	—	22	25
" 25	25	26	23	24	26	24	24	—	24	26
" 26	25	—	24	24	—	24	25	—	24	—
" 27	25	—	26	25	—	26	26	—	24	—
" 28	25	—	—	25	—	—	—	—	24	—
" 29	25	—	—	25	—	—	—	—	24	—
" 30	26	—	—	26	—	—	—	—	24	—
" 31	—	—	—	—	—	—	—	—	24	—
August 1	—	—	—	—	—	—	—	—	25	—
" 2	—	—	—	—	—	—	—	—	26	—

Seedlings. The flowering stems were cut before seed could have been formed in 1932, but they were left till late autumn in 1933. No good seed has been found in diploid spikes at Potterne or Kew and no seedlings have appeared on the beds. The clone is obviously self-sterile and on none of the beds did crossing with the hexaploid (at least as pollen parent) occur. It may be noted that, excluding secondary shoots, the flowering periods of the two "types" have not overlapped at Potterne.

Phleum pratense*—hexaploid.Deaths.* No. 61 on clay (June-July 1932).

No. 81 on chalky clay (winter 1932-3).

General tone.

6. vi. 32	11. vii. 32	15. viii. 32	20. ix. 32	27. xii. 32
Potterne soil	Potterne soil	Potterne soil	Potterne soil	Potterne soil
Clay	Calcareous sand	Clay	Clay	Clay
Calcareous sand	Sand	Sand	Sand	Chalky clay
Chalky clay	Clay	Chalky clay	Chalky clay	Sand
Sand	Chalky clay	Calcareous sand	Calcareous sand	Calcareous sand

Throughout 1933 the same sequence as for 27. xii. 32 was maintained.

Secondary shooting occurred, after browning of old leaves, on all plots, but little from the very dense clumps on Potterne soil.*Number of stems, stem heights, number and length of internodes, and spike lengths.*

The results of analysing all the stems and spikes of all the ramets of *P. pratense* hexaploid of the main (first) cutting for 1932 are given in the following four tables. We wish to express our indebtedness to Mr A. K. Jackson for assistance in the scoring and to Mr H. Montford, B.Sc., for the statistical analyses.

Stem count per ramet.

Soil	Max.	Min.	Mean	Standard error of mean	Standard deviation	Coefficient of variation
Sand	20	8	13.8	±0.68	3.45	0.25
Calcareous sand	21	6	10.2	±1.00	5.10	0.50
Clay	27	8	15.0	±1.12	5.58	0.37
Chalky clay	12	2	7.2	±0.67	3.42	0.48
Potterne soil	37	16	27.0	±1.14	5.81	0.22

Stem height in cm.

Soil	Max. (absolute)	Min. (absolute)	Mean per ramet	Standard error of mean	Standard deviation	Coefficient of variation
Sand	122	38	87.6	±1.1	5.70	0.065
Calcareous sand	124	36	89.8	±1.2	6.03	0.067
Clay	114	29	76.3	±1.3	6.71	0.088
Chalky clay	119	46	81.7	±1.1	5.74	0.070
Potterne soil	138	53	106.2	±1.3	6.88	0.065

Number of nodes.

Soil	Max. (absolute)	Min. (absolute)	Mean per ramet	Standard error of mean	Standard deviation	Coefficient of variation
Sand	6	1	2.99	±0.04	0.22	0.073
Calcareous sand	5	1	3.35	±0.03	0.17	0.051
Clay	5	0	2.61	±0.03	0.16	0.061
Chalky clay	5	1	2.98	±0.06	0.30	0.101
Potterne soil	6	1	3.27	±0.05	0.24	0.073

Length of fruiting spike.

Soil	Max. (absolute)	Min. (absolute)	Mean per ramet	Standard error of mean	Standard deviation	Coefficient of variation
Sand	148	27	59.3	±0.95	4.85	0.082
Calcareous sand	201	32	68.8	±1.31	6.67	0.097
Clay	220	12	73.1	±1.28	6.42	0.088
Chalky clay	185	30	72.1	±2.15	10.95	0.152
Potterne soil	210	22	73.3	±0.83	4.25	0.058

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The stems were cut off immediately above the lowest node of the flowering stem.

After the fruiting stems had been cut in 1932 all the ramets produced a variable number of secondary stems which either succeeded in elongating and producing inflorescences or were prevented completing their growth by autumnal frosts. These secondaries were removed in three subsequent cuttings and the total counts for these were: sand 273, calcareous sand 189, clay 381, chalky clay 237, Potterne soil 467.

For 1933, the following tables give the results of the analyses:

Number of stems per ramet.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Maximum	63	27	111	85	147
Minimum	23	10	48	24	41
Mean	38.3	17	75.1	47.8	98.5
Standard deviation	9.8	4.9	19.5	13.1	29.5

Longest stem length per ramet in cm.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Maximum	112	105	145	130	142
Minimum	102	90	120	97	122
Mean	108.1	97.5	132.1	117	135.1
Standard deviation	3.2	4.8	6.8	9.8	6.4

Shortest stem length per ramet in cm.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Maximum	90	75	90	85	97
Minimum	32	37	42	30	60
Mean	64.4	65.1	70.1	57.2	79.5
Standard deviation	11.7	8.2	9.3	13.3	11.9

First flowering.

	1932					1933				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
June 27	—	—	—	—	—	11	6	5	7	—
„ 28	—	—	—	—	—	11	6	6	12	—
„ 29	—	—	—	—	—	25	8	6	12	—
„ 30	—	—	—	—	—	26	26	25	25	25
July 1	—	—	—	—	—	—	—	—	—	26
„ 2	—	—	—	—	—	—	—	—	—	—
„ 3	—	—	1	4	—	—	—	—	—	—
„ 4	—	—	1	5	—	—	—	—	—	—
„ 5	1	5	5	17	1	—	—	—	—	—
„ 6	3	15	13	24	2	—	—	—	—	—
„ 7	3	15	14	24	2	—	—	—	—	—
„ 8	24	26	25	25	23	—	—	—	—	—
„ 9	25	—	—	25	23	—	—	—	—	—
„ 10	26	—	—	26	26	—	—	—	—	—

All ramets had completed their flowering, i.e. all pollen had been shed, by 11. vii. 33, before any of the ramets of *P. pratense* diploid had commenced flowering.

Seedlings. The flowering stems were cut before seed fell in 1932. In 1933 good seed was set by plants and fell on all soils, i.e. the clone is self-fertile. Seedlings appeared as follows: sand, many; calcareous sand, many; clay, many; calcareous clay, numerous; Potterne soil, very numerous. 1933 seed from one plant on every plot was sown in Potterne soil on October 28th, 1933 and showed excellent germination by November 19th, 1933.

SUMMARY AND TENTATIVE CONCLUSIONS.

1. Figures for rainfall, temperature, and humidity are given for 1932 and 1933. The only exceptional feature was the low rainfall for 1933, with the absence of thunderstorms, yet with high temperatures.

2. The results of periodic records of the seven species now in position for the two years are embodied in this report. The chief facts which have emerged are:

Centaurea nemoralis. This species continues to maintain itself as a persistent perennial. Only thirteen deaths (all soils) have occurred, out of 130 plants, in six years, all except one on clay and Potterne soil. No deaths have so far been recorded on sands. No morphological differences between the ramets on the soils have appeared. Fairy-ring-like growth has increased. The habit differences between the ramets (of one and the same clone) at Kew (stems widely ascending) and Potterne (stems erect) has been maintained for six years. The number of flowering stems was greatest on the calcareous sand and least on the clay. On every soil the absolute number and the mean increased from 1932 to 1933. The standard deviation decreased on the sand but increased on all the other soils. The effect of competition between the outer and inner rows of ramets is very clearly shown in a special table and diagram.

Silene maritima. The original transplant stock has died out so that only eight original plants are now alive, on all soils. One of the originals is being cloned and it is hoped to replant in 1935. On clay many main roots spread horizontally a short distance below the surface. On the sand and calcareous sand the roots penetrated nearly vertically. On the Potterne soil they were much coiled immediately below the root-stock. The superficial cells of the older roots were coloured differently in the various soils.

Anthyllis vulneraria. No morphological changes of a qualitative nature occurred. This negative result has now been obtained with three generations (six years). In seedling stages and during the first year of growth the plants have again done best on Potterne soil but during the second year the plants on calcareous sand showed best tone but were second to those on Potterne soil for number of stems per plant. Continuous seed germination throughout the year, except during hard frost, is confirmed. Two samples of wild populations were analysed for certain characters and the results compared with growth on the Transplants. It is shown that grazing and competition with other vegetation reduce potential growth enormously.

Plantago major L. The very great differences between the plants on the various soils have been maintained. Plants on the sands have remained very small, those on the clay and Potterne soil are large and luxuriant. The plants on the chalky clay have somewhat decreased in size, probably owing to biotic factors. Persistence of original plants has also been most marked (24 out of 26) on the clay. The peculiar fluctuations between a strict and a flat habit have been recorded in considerable detail, but the cause remains unknown. Seed germination is continuous from spring to autumn. Indumentum differences were again noted. The number of flowering spikes was higher on every soil in 1932 than in 1933; it was very much the highest on clay and lowest on calcareous sand. The differences between the soils was highly significant. The standard deviations increased only on clay and Potterne soil.

Fragaria vesca has established itself well on all the soils. It has obviously flourished best on Potterne soil and clay. It has done worst on chalky clay, except for fruit size. Immediate, continuous, and delayed types of germination were recorded. On clay some seeds germinated while fruits were still attached to the parent plant. Most seedlings were recorded on Potterne soil and clay. The greatest stem heights and number of runners were recorded for Potterne soil, the least for chalky clay. The number of runners increased from 1932 to 1933 on all soils except sand and chalky clay. The standard deviation increased on every soil.

Phleum pratense—*diploid*. The plants have become well established on all soils and no deaths have occurred. For general tone and luxuriance and number of stems, they have done best on Potterne soil and worst on calcareous sand. For longest stem length Potterne soil has the highest mean and clay the lowest. For maximum spike length Potterne soil has the highest mean and sand the lowest. The analyses of a very large number of counts and measurements clearly indicate these and other differences which are relatively great considering that the plants have been in position less than two years. The stock is self-sterile.

P. pratense—*hexaploid*. The plants have become well established on all soils and only two deaths have occurred. For general tone and luxuriance they have done best on Potterne soil and worst on calcareous sand. Analyses, made of a very large number of counts and measurements, clearly indicate the differences. The stock is self-fertile and seedlings appeared on all soils.

The very considerable differences (morphological and physiological) between the two "types" of *Phleum* have been maintained on all the soils. There has been no sign of approximation in habit or other characters. They have, however, reacted, on the whole, in a relatively similar manner on every soil.

3. Moss growth was again most pronounced on calcareous sand and the slug population greatest on clay. The latter had to be artificially controlled.

4. Primary flowering has been carefully recorded for all species except *Silene maritima*. In *Centaurea nemoralis*, *Plantago major*, *Fragaria vesca*, and

Phleum pratense hexaploid, first flowering (and for *F. vesca* first fruiting) was much earlier in 1933 than in 1932. The differences between the two years were very striking. In *Anthyllis*, plants on chalky clay were the last to commence and the last to complete first flowering. First flowering was completed first for both years in *Plantago major* on clay. In *Phleum pratense* diploid there was little difference in time of first flowering between 1932 and 1933.

5. In this third report of the B.E.S. Transplant experiments the results have been given in a somewhat more quantitative form than in the earlier reports. This should make final comparison easier and has already enabled differences to be expressed clearly and concisely and with a minimum of repetition. On the other hand, qualitative variations of considerable biological interest continue to be recorded.

THE VEGETATION OF FOOTPATHS, SIDEWALKS, CART-TRACKS AND GATEWAYS

By G. H. BATES.

(With Plates XXXV–XXXVII.)

I. FOOTPATHS.

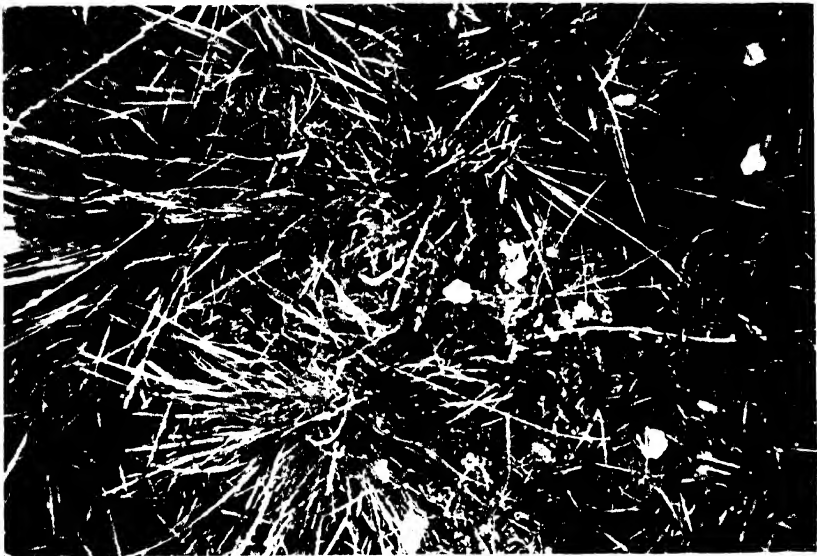
THE contrast between the vegetation of footpaths traversing grassland and that of the surrounds has been commented upon by observers on numerous occasions, while graziers have recognised the fact that horses and sheep prefer to feed upon the footpath rather than the other parts of the field. Apart from a passing speculation by Darwin ((1), p. 10), no detailed examination of conditions or of the factors concerned appears to have been made, in spite of the possibility of the findings being of economic value.

The vegetation of the path is usually shorter than that of the surrounding areas, though this varies with the intensity of grazing. The most outstanding phenomenon is the dark green colour of the path in comparison with the other herbage. This deep colour is maintained throughout the year and is most conspicuous in winter when the path stands out in vivid contrast to the dead remains of plant life on each side.

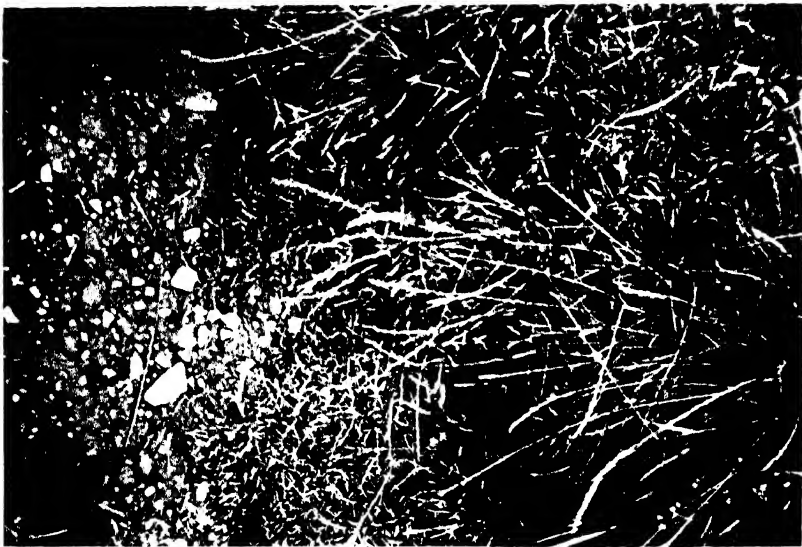
With the exception of paths on very dry sandy soil, the dominant species are smooth-stalked meadow grass (*Poa pratensis*), perennial rye grass (*Lolium perenne*) and wild white clover (*Trifolium repens*). *Poa pratensis* is constant for all examples and *Lolium perenne* for the majority. *Trifolium repens* is extremely scarce in shaded positions, but is constant for all paths exposed to sunlight. Crested dogstail (*Cynosurus cristatus*), cocksfoot (*Dactylis glomerata*) and plantains (*Plantago* spp.) are fairly constant.

A distinct and constant zonation is found. In the centre of the path, if much used, is an area of bare earth. This is adjoined on either side by a zone of *Poa pratensis* followed by zones of *Lolium perenne* and *Trifolium repens*. An example is shown in Pl. XXXV, phot. 1, this being a path on a Lakeland fell. The surrounding vegetation is an *Agrostis-Festuca* association with *Briza media*, *Vaccinium myrtillus*, *Molinia caerulea* and *Nardus stricta* as sub-dominants. Pl. XXXV, phot. 2 shows a small area of this and is a typical example of the contrast which occurs.

On dry sandy heaths in districts of low rainfall the dominant species of the path are usually *Festuca ovina*, *Agrostis stolonifera*, *Galium* spp., *Plantago* spp. and *Hieracium* spp. On heavier soils and in moister situations, where puddling of the surface occurs in winter, it is notable that areas dominated by *Poa*



Phot. 2. Herbage on steep hillside adjoining footpath. Plants present are *Molinia caerulea*, *Agrostis stolonifera*, *Festuca ovina*, *Vaccinium myrtillus* and *Potentilla erecta*.



Phot. 1. Zonation on edge of footpath.

Bare
ground

Poa
pratensis

Trifolium
repens

Lolium
perenne

pratensis and *Lolium perenne* are those where the surface is disturbed. The sward is not broken, but the mud oozes through and almost covers the surface.

Footpaths are obviously of varying lengths but the width is limited according to circumstances and may vary from a few inches, as on a mountain side, to several yards, as on a common. The lateral boundaries are not sharply defined, but merge gradually into the surrounds, for treading is not evenly distributed and is more concentrated in the centre. The boundary usually occurs where the *Lolium perenne* and *Trifolium repens* zone reaches its outer limit.

Floristic composition of the vegetation of footpaths.

The above statements with regard to the floristic composition of footpath vegetation and the arrangement of species into zones is so patent to everyday observation that elaboration in the form of statistical data is scarcely necessary.

To provide some illustration, however, eight examples are taken as follows:

Example 1. Sheep Walk. Tarn Hows, Lancashire.

„ 2. Larch Wood, Gooseyfoot Tarn, Lancashire.

„ 3. Mixed Wood, Walton, Derbyshire.

„ 4. Paddock, Ashgate, Derbyshire.

„ 5. Marsh Pasture, Terrington Marsh, Norfolk.

„ 6. Riverside, Gaywood, Norfolk.

„ 7. Chalk Heath, Massingham Heath, Norfolk.

„ 8. Sandy Heath, Wooton Heath, Norfolk.

Example 1 occurred on a hillside where the soil was very acid (pH 4) and the rainfall high. Example 2 occurred under similar conditions but in a shaded situation. Example 3 occurred on a medium loam with an acid reaction (pH 5). Example 4 occurred in the same neighbourhood as Example 3, but the soil was neutral in reaction owing to heavy liming. All forms of grazing animals, including rodents, were excluded from this site. Example 5 is found upon a pasture of renowned grazing value on the silt land bordering the Wash. Example 6 was upon a black alluvial riverside soil, neutral in reaction. Example 7 was that of a footpath traversing a heath overlying chalk, the soil being comparatively moist and neutral in reaction. Example 8 occurred upon a dry, sandy, acid heath (pH 5) overlying a Lower Greensand formation.

An intensive survey of the above examples was carried out both in summer and in winter. Quantitative data, both of areal percentage occupied and of frequency, were collected both from the footpath proper and also for comparative purposes from the surrounds. Qualitative data relating to constancy, exclusiveness, vitality and periodicity were obtained from 100 examples.

For the purposes of this article the publication of the whole of this information would be superfluous, and, as already stated, the phenomena are familiar or are easily accessible to the observer. For the purposes of the subsequent examination of the problem, however, the findings are summarised below.

Quantitative data.(1) *Areal percentage.*

In all the eight examples bare ground occurred where treading was most severe, and occupied an average of approximately 18 per cent. of the ground covered by the path.

Poa pratensis occupied an average of 34 per cent. of the area of the paths in Examples 1-8, but only 2 per cent. of the area in Example 8 on dry sandy heath.

Lolium perenne occupied an average of 18 per cent. of the area of the paths in Examples 1-8, but only 1 per cent. in Example 8 and was absent in Example 2.

Trifolium repens occupied an average of 10 per cent. of the area of the paths in Examples 1-8, but was absent in Example 2 and only covered 2 per cent. of the area in Example 8.

Plantago spp. and *Bellis perennis* were present in two examples, and other species such as *Dactylis glomerata* and *Cynosurus cristatus* were present in others.

Poa pratensis, *Lolium perenne* and *Trifolium repens* were the dominants on the paths on which they occurred.

In all cases except Examples 5 and 8, the flora of the surrounds was mixed and none of the above species were dominants. In Example 5, however, *Poa pratensis*, *Lolium perenne* and *Trifolium repens* were co-dominants on the surrounds as well as on the path, and in Example 8 both the path and the surrounds consisted of an *Agrostis-Festuca* association containing *Galium saxatile* and *Plantago coronopus* as sub-dominants.

(2) *Frequency.*

This was determined by noting the number of times a species or a patch of bare ground occurred within a 10 × 10 in. quadrat frame thrown 100 times at random.

Bare ground occurred with an average frequency of 33 per cent. over the eight examples. *Poa pratensis* had an average frequency of 69 per cent., *Lolium perenne* 55 per cent. and *Trifolium repens* 35 per cent. over the eight examples. No other species possessed a frequency of any magnitude in comparison with the above. None of the above species displayed a high frequency on the surrounds except again in Example 5, where *Poa pratensis*, *Lolium perenne* and *Trifolium repens* were high and in Example 8 where *Agrostis* spp. and *Festuca ovina* had the highest frequency.

(3) *Constancy.*

Both *Poa pratensis* and *Lolium perenne* displayed 100 per cent. constancy upon paths, while *Trifolium repens* displayed 80 per cent. constancy. No other species was comparable with the above, the next in order being *Galium saxatile* 32 per cent., and *Bellis perennis* 25 per cent.

Qualitative data (from 100 examples).

Exclusiveness. No species could be described as exclusive to the footpath, but the following are preferential: *Poa pratensis*, *Lolium perenne*, *Trifolium repens*, *Bellis perennis*, *Hieracium* spp., *Plantago major* and *P. coronopus*.

Vitality. The following species regularly accomplish their complete life cycle: *Poa pratensis*, *Lolium perenne*, *Cynosurus cristatus*, *Trifolium repens*, *Galium saxatile*, *Plantago* spp. and *Luzula* spp. Many other species found on the paths only showed vegetative development.

Periodicity. The following species only were winter green: *Poa pratensis*, *Lolium perenne* and *Cynosurus cristatus*. Other species were dormant during the winter months.

Habitat factors.

(1) *Edaphic factors.*

General physical conditions. The soil of the footpath is in the first place similar to that of the surrounds, and would exhibit the same characters upon mechanical analysis. Any differences in the physical condition of the soil between path and surround are the result of treading upon the path.

It is obvious that the soil of the path possesses a greater density than that of the surrounds, and this has a secondary influence upon temperature and moisture conditions. Attempts to obtain definite measures of the respective densities were a failure and only approximations were possible. This was due to the difficulty of exact excavation, owing to plant roots and to stones. Several facts were, however, quite apparent from the investigation.

In the surrounds the top 5 cm. were of lower density than those below, owing to the lightening effect of plant roots, and also to the fact that there is no superimposed layer of soil, and that no treading occurs. On the footpath the surface soil is of greater or equal density to the lower soil. The lower soil of the paths was of about the same density as that of the lower soil of the surrounds.

It would appear that in the case of the footpath, the denser or consolidated condition of the soil, due to treading, exists only in about the first 3–5 cm., and that below that level conditions are comparable with those at a similar depth in the remainder of the field.

The exact arrangement or texture of the particles in the surface layer will differ according to whether the trodden soils contain a certain proportion of clay or not. Clay when trodden or “puddled” in the presence of moisture becomes altered physically, owing to deflocculation of the particles. The result of this action is the retention of moisture on the soil surface, and upon the soil drying by the evaporation of this moisture, a “baked” or “poached” condition arises, and a hard, “baked” crust of varying thickness is formed.

The proportion of clay in the soil of the footpath and the condition arising therefrom cannot be of any importance as a factor influencing the constitution

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of the footpath community, for the community is the same in its main features on other types of soil, except in the extreme case of dry sandy heath.

Experiments were carried out in 1929 ((2), p. 587) on a heavy loam soil (Chesterfield, Derbyshire), and again in 1932 on light sandy loam (near King's Lynn, Norfolk) in an attempt to determine whether consolidation in itself exerted direct influence or selective influence on the species. A garden border was in each case divided into two, one half being consolidated and the other left loose. The following species were sown in rows (duplicated and randomised) across both loose and solid areas: *Lolium perenne*, *Poa pratensis*, *Holcus lanatus*, *Agrostis stolonifera*, *Festuca ovina*, *Trifolium repens* and *Plantago major*.

In the case of the 1929 experiment soil was consolidated to a depth of about 30 cm., by packing the soil layer upon layer. In this experiment it was found that all the species were reduced to about half the size and weight of those upon the loose soil. The root systems were also restricted by the solid soil.

In the 1932 experiment consolidation was carried out by surface pressure after the species were established, care being taken not to crush any of the leaves or stems of the plants. In this case the consolidation resembled the type effected on the footpath, i.e. only the first few centimetres of soil were affected. In this experiment little result was noted, except in the case of *Poa pratensis* which was reduced in size in the consolidated portion. *Holcus lanatus*, *Agrostis stolonifera* and *Festuca ovina* were slightly stunted. It is significant that these species are comparatively shallow-rooted.

From the above results there appears no reason to suppose that consolidation itself is responsible for the "footpath flora". *Poa pratensis* is the species most adversely affected, and yet this is the constant and most abundant species upon the consolidated portion of a path.

Soil moisture. On the whole the footpath is a moister habitat than the surrounds. The pressure of the soil particles into closer association should increase surface tension and consequently the power of a soil to retain moisture, though in recently published work (3) it has been shown that consolidation does not greatly affect water-holding capacity. The surface of the footpath, however, is pressed down to a lower level than the surrounds and gravitation will increase water supply in virtue of this fact. Another factor is that the vegetation of the surrounds is frequently matted, and this surface covering of root material retains water at the surface and renders the soil dry. On the footpath "mat" is eliminated by treading and a freer access of water is possible.

On the other hand a clay soil may, in the puddled state of the footpath, prohibit the access of moisture, and may bake very hard in dry weather. Moisture conditions will be worse, in such cases, on the path than on the surrounds, yet the footpath still possesses its distinctive vegetation.

The species of the footpath socies are not, as a whole, characteristic of a wet or dry habitat. *Lolium perenne* thrives under good moisture conditions, but is

deep rooted and fairly drought-resistant. *Poa pratensis* is shallow rooted, but possesses underground runners and is drought-resistant. This latter grass is recognised by agricultural botanists as one that tolerates dry situations. *Trifolium repens*, in virtue of its deep root system, is very drought-resistant, and it is often to be observed that when pastures are burnt dry, this species is still present in a green state. Actually a dry season favours the development of *Trifolium repens*.

In view of the above facts it does not appear that moisture in itself can be regarded as a factor which is directly responsible for the existence of a distinct footpath socies. It is asserted by some that the distinct green colour of the footpath in winter is due to moisture, but this may be explained by the fact that the species of the footpath are all winter green.

It is to be observed that the footpaths existing on dry sandy soil in districts of low rainfall do not possess the characteristic flora of paths in other situations (Example 8). Small colonies of *Poa pratensis* and *Lolium perenne* may be found in the damp hollows, but the dominant and subdominant species are *Festuca ovina*, *Agrostis stolonifera*, *Galium* spp., *Plantago* spp. (excluding *Plantago major*) and *Hieracium* spp. The phenomena were also noted where paths traversed a cinder track and a slag heap (4).

On all other types of soils in moister situations the characteristic footpath community exists on an area which coincides exactly with that which is puddled on the surface in winter. As already stated, the sward is not broken, but mud oozes through and becomes mixed with the herbage. The occurrence of the typical footpath community of *Poa pratensis*, *Lolium perenne* and *Trifolium repens* on puddled areas is highly significant and goes to show that a moist condition of the soil is important, though certainly an indirect factor. The presence of moisture and a suitable physical condition of the soil are essential to puddling. *Poa pratensis* and *Lolium perenne* can tolerate puddling, which is thus essential to the production of the footpath socies, because, as will be seen later, it is lethal to species not characteristic of the footpath.

Chemical composition. There is no reason why the chemical composition of the soil of the footpath should vary from that of the surrounds. There is in some cases a greater accumulation of organic matter from decayed vegetation on the surrounds than on the footpath, but this is not always the case. It is also notable that grazing animals prefer the footpath, and thus it may receive more droppings and urine than the surrounds. It is to be noted, however, that in the case of some paths, livestock and even rabbits are excluded, e.g. Example 4.

As regards soil acidity a number of investigations failed to reveal any significant difference in the pH value of the soil of the surrounds and the path, except where much "mat" was present on the surrounds, and here a difference was recorded, the earth below the "mat" being more acid than that of the path.

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Light and aspect. Where a footpath traverses grassland there is a greater illumination on the path than on the surrounds, owing to the fact that the herbage is suppressed by treading, and its shading effect thereby removed. In many cases where a path runs from east to west the north margin of the path (which faces south) will be illuminated by the direct rays of the sun at its maximum intensity. The opposite side, especially where overshadowed by tall grass or raised ground, will be shaded. The difference in illumination determined by actinometer was for the shaded portion one-ninth that of the lighted northern side, in a typical example.

Light intensity exerts a marked influence upon *Trifolium repens*. In a shaded habitat, such as a wood or where other objects exclude sunlight, *Trifolium repens* is absent or very scanty, e.g. Example 2. Even aspect affects this species, and it will be found that where the southern side of a path is shaded from direct sunlight by tall grass or rising ground there is a considerably lower scale of abundance, frequency and dominance than on the opposite side. When *Trifolium repens* is in flower, the relative abundance of white flower-heads on the side of a path with a southern aspect compared with the shaded northern aspect on the opposite side is very conspicuous. Light intensity does not appear to exert any marked influence on the other species of the footpath, and they may all be found in shaded situations.

The influence of the biotic factor.

Grazing. It is notable that livestock prefer to graze the footpaths rather than the surrounds. This applies mostly to sheep and horses, as these animals bite closely. It must be obvious upon consideration that grazing is a secondary influence. The species of the footpath are the best pasture plants in the agricultural sense, and owing to their shortness they offer a succulent herbage. The droppings and urine from the animals are sometimes held responsible for the green colour of the path, as is the case with water supply. No difference is noted, however, on footpaths where grazing animals, including rabbits, are excluded, e.g. Example 4.

Treading. The effect of treading upon the flora of a community is threefold, and is both direct and indirect. The indirect action has already been studied, i.e. the consolidation of the soil and its influence upon the species. It has been shown that this is not responsible for the footpath socies.

The direct influences are those of treading and puddling upon the plant itself, and the mechanical effect or injury caused thereby. It is very obvious that many species are damaged and are often completely destroyed by the action of treading, while on the other hand the species of the footpath socies are comparatively immune to harm of this kind. The reason for this immunity or resistance must obviously be due to some peculiarity of structure which the species possess in common, and which is not possessed by the species susceptible to injury.

An examination of the habit of growth of the dominant gramineous species *Poa pratensis* and *Lolium perenne*, shows a very striking and significant character possessed by these species and not by the species of the surrounds, i.e. the conduplicate stem and folded leaf section as compared with the rolling of the leaf in other Gramineae (excepting *Poa* spp., *Dactylis glomerata* and *Cynosurus cristatus*). An examination of this structure of leaf and stem shows it to be an excellent adaptation to resist injury, for the leaf and stem offer a flat surface to the crushing action of the foot. The conduplicate arrangement of the shoot is of similar mechanical structure to the leaf springs of a carriage.

The life form of the gramineous species of the footpath is also distinct from that of the most frequent species of the surrounds. The gramineous species of the path constitute a synusia of cryptophytes, the buds being buried just below the level of the soil. The Gramineae of the surrounds are mainly hemicryptophytes, the buds being at ground level, and two of the species, *Agrostis* spp. and *Holcus mollis*, may be chamaephytes.

The arrangement of the gramineous species into life forms is a somewhat fine point. It might be argued that some species described in this thesis as cryptophytes or chamaephytes respectively might all be grouped as hemicryptophytes, but adhering rigidly to the position of their perennating organs as the criterion, there is no doubt as to which species tend to the cryptophytic habit and which to the chamaephytic.

It appears obvious that the double adaptation, i.e. the folded leaf and the conduplicate stem with the cryptophytic life form, enable the plant to withstand injury. The leaf and stem are resistant to injury, while the growing point is protected below the surface of the earth.

It has been noted that *Poa pratensis* occupies the zone of the most intense treading and is followed by *Lolium perenne* on the less trodden area. A comparison of the two species shows *Poa pratensis* to be better adapted than *Lolium perenne* to resist injury. In the former case the growing point is buried deeper in the soil and the plant propagates by underground stolons as well as by seed. The leaves of *Poa pratensis* are short, tough and concave in longitudinal and cross section. The leaves of *Lolium perenne* are longer and more flaccid.

It is notable that *Poa trivialis*, though possessing much the same foliage characters as *P. pratensis*, is very rare on the well-trodden portion of footpaths. This species is definitely chamaephytic in life form. It has also been noted that *P. annua* may occupy interstices where it is protected from treading, and it may also have a transient existence where treading is for some reason suspended ((2), p. 589). *P. annua* is a therophyte.

Of the non-gramineous species *Plantago major* is well adapted to withstand treading. The leaves are broad and tough and occur in rosette form, the upper ones protecting the lower. On the footpath the plant is an ecad occurring here as a cryptophyte, whereas on untrodden areas it is a hemicryptophyte with semi-erect leaves. The average size of the plant is smaller on the footpath than

on the surrounds. Similar phenomena are noted in the case of *Plantago media*, *P. lanceolata* and *P. Coronopus*.

Trifolium repens is least adapted to treading of any of the footpath species, and it is a significant fact that it occupies the outer zone and invades the footpath from the surrounds. Light appears to offer the greatest stimulus to this species and to account for its presence on the footpath. The plant is a chamaephyte with prostrate runners, and in virtue of the tough and prostrate nature of these runners exhibits a certain resistance to treading. The leaves are often injured by the process and are smaller in size upon trodden area (4). *Trifolium repens* is not injured by even pressure (as contrasted with treading) to the same extent as are the Gramineae.

Experiments upon the influence of treading.

An experiment was carried out to test the theory of resistance to injury possessed by certain species and not by others ((2), p. 589). The following grasses were grown in separate and repeated strips: *Poa pratensis*, *Dactylis glomerata*, *Lolium perenne*, *Anthoxanthum odoratum*, *Alopecurus pratensis* and *Agrostis vulgaris*. The ground was then utilised as a garden path and trodden daily. *Poa pratensis* assumed a low dense habit, *Dactylis glomerata* and *Lolium perenne* were suppressed but persisted. The three remaining species were exterminated by treading. The experiment was carried out in 1929 on a heavy loam (Chesterfield, Derbyshire). Puddling took place during wet weather, though the work was carried out in summer.

A further experiment was carried out on a light loam (King's Lynn, Norfolk). The following species were sown in rows and the trial duplicated. *Trifolium repens*, *Dactylis glomerata*, *Poa pratensis*, *Lolium perenne*, *Festuca elatior*, *Agrostis stolonifera* and *Agropyrum repens* (the latter was planted in the form of runners). A pathway was trodden through the plots and the species were subjected to a severe treading and puddling during a wet summer and autumn.

Trifolium repens was affected by the treading but not destroyed. *Dactylis glomerata*, *Poa pratensis* and *Lolium perenne* were somewhat restricted in development but persisted and quickly recovered from the bruising action of treading by making fresh growth during the resting stage. *Festuca elatior* offered some resistance, but eventually the buds in the centre of the plant, being above ground level, were destroyed. *Agrostis stolonifera* and *Agropyrum repens* were completely destroyed and in the latter case the runners appeared dead and shrunk.

It was noted that seedlings of *Poa pratensis* appeared all over the trodden areas, but were very dense in the region of the *P. pratensis* strips. It is possible that some of the seedlings were those of *P. annua*, but if so they did not persist beyond the seedling stage, as no mature plants were identifiable.

The exact effect of treading was as follows: The original plants were broken

down, and the leaves damaged in the case of all the species. In the case of *Festuca elatior*, *Agrostis stolonifera* and *Agropyrum repens* the buds at the base of the plants were trampled in the mud and damaged, but with *Dactylis glomerata*, *Poa pratensis* and *Lolium perenne*, these were protected beneath the surface of the soil. It appeared that the damage to the bared buds of *Festuca elatior*, *Agrostis stolonifera* and *Agropyrum repens* only took place when the earth was wet and treading produced a pulpy condition.

Special influence of treading.

Festuca ovina and *Agrostis stolonifera* appear capable of withstanding treading upon a dry footpath, but they do not tolerate puddling. The same applies to *Galium* spp. These plants are extremely stunted by the treading and the leaves are very fine. It is obvious that the stunted leaf of *Agrostis* and the setaceous leaf of *Festuca ovina* must be resistant to treading, and it is significant that these species are the dominants on dry footpaths. Many other cryptophytic species occur on the surrounds, but are not found on footpaths, and are all of a type which would be damaged by treading, i.e. upright or fragile.

While *Festuca ovina* and *Agrostis stolonifera* are able to withstand treading upon the leaf they are not able to withstand the slight surface disturbance caused by puddling, and the damage done by the bruising action of the foot or hoof when pressing into the surface soil. These two species are chamaephytes and their growing points are on the surface of the earth: furthermore they possess an extremely superficial root-system, forming a mat of root material at their base.

Large-scale experiment on the influence of puddling.

An experiment was carried out on a large scale in Hardwick Park, Derbyshire, illustrating the effect of puddling upon an association of *Agrostis* and *Festuca* (5). The aim was to imitate the action of the hoof in wet weather on about four acres of very matted grassland. The composition of the grassland, assessed on the percentage area basis, was:

<i>Agrostis</i> spp.	35.4
<i>Cynosurus cristatus</i>	24.6
<i>Festuca ovina</i>	23.1
<i>Luzula campestris</i> (agg.)	9.2
<i>Lolium perenne</i>	7.7
<i>Trifolium repens</i>	
<i>Ranunculus</i> spp.	
Moss	
<i>Holcus lanatus</i>	
	<hr/> 100.0

The sward was cut frequently in two directions by a disc harrow, drawn by a tractor while the ground was very wet and rain was falling. The turf was worked into a morass of mud and presented a puddled appearance. It was then heavily rolled. The operation was carried out in March 1929, and in the following summer a complete change in the flora was noted. The analysis of the treated portion was then as follows:

<i>Poa pratensis</i>	50.9
<i>Cynosurus cristatus</i>	21.7
<i>Agrostis</i> spp.	9.1
<i>Trifolium repens</i>	12.0
<i>Lolium perenne</i>	1.0
<i>Holcus lanatus</i>	5.3
<i>Festuca ovina</i>	
<i>Ranunculus</i> spp.)	
	<hr/> 100.0

The analyses of the herbage were carried out independently by Mr A. Roebuck of the Midland Agricultural and Dairy College.

The influence of this puddling action, carried out on a large scale, shows a result of such striking similarity to that observed on the footpath, as to need no elaboration. The astonishing acquirement of dominance by *Poa pratensis* in so short a time must be explained by very widespread presence of the seed over the area and the establishment of a peculiarly favourable seedbed by the "puddling" operation. The plants were young when examined in the summer, and hay had previously been fed to cattle on the area. As will be seen, the *Poa* mainly replaced *Festuca* and *Agrostis*, which were severely reduced.

It would appear probable that the evergreen or "winter green" condition of *Poa pratensis* and *Lolium perenne* may be a factor in their favour in the footpath community, in that they are in a growing state during the puddling process. This may exert some influence, but in the above experiment, the time of the operation (i.e. March in a moist warm spring) allowed a good chance for *Festuca ovina* and *Agrostis stolonifera* to recuperate.

Selective influence of treading and puddling.

From a consideration of the above data it would appear that the species which are found on footpaths, in wet or dry situations, are enabled to persist by virtue of their leaf structure. When, however, puddling becomes a factor, *Festuca ovina* and *Agrostis stolonifera* are obliterated, but all species possessing the cryptophytic life form are able to persist.

The influence of treading and puddling upon a gramineous community may be readily demonstrated by rubbing a given area with a rubber squeegee during wet weather or when the ground is in a wet condition. An experiment of this nature was carried out on Massingham Heath, Norfolk (August 1932). Three quadrats were chosen, each 1 sq. metre in area, with *Agrostis stolonifera*, *Festuca ovina*, and *Holcus lanatus* as co-dominants, and scattered individuals of *Lolium perenne*, *Trifolium repens* and *Plantago* spp. The areas were rubbed with a squeegee and with the foot until the vegetation was bruised and the surface pasted with mud. Several days later it was noted that the quadrats presented, as a whole, a dead appearance. It was observed, however, that while *Agrostis stolonifera*, *Festuca ovina*, and *Holcus lanatus* were apparently dead, the "stumps" of *Lolium perenne* and *Plantago* spp. stood out of the ground in a striking manner and were still green. The runners of *Trifolium*

repens also remained green. A fortnight later it was noted that some of the *Agrostis stolonifera* showed signs of recovery, a few fresh green shoots having arisen, but *Festuca ovina* had not recovered and *Holcus lanatus* was obliterated beyond recognition. *Lolium perenne* had made a good recovery, having grown leaves up to 10 cm. long. *Trifolium repens* was developing leaves and so was *Plantago* spp.

The formation of the footpath socies.

In the years 1929-30, in a grass paddock (Hawkshead Hill), attempts were made to study the formation of a footpath socies, by observations carried out on several areas when the footpath was diverted to fresh ground. Permanent quadrats were unfortunately obliterated, but the following facts were revealed from close observation.

Existing species not typical of the footpath synusia were suppressed and bare ground populated by *Poa pratensis* which in some cases sprang from seed, but in others proliferated from pre-existing individuals. *Plantago* spp. also appeared as seedlings upon this central area and grew to maturity. *Lolium perenne* did not appear as seedlings in the first place, but pre-existing specimens persisted and proliferated, and in the second year seedlings were observed. *Trifolium repens* invaded the outer margins of the path vegetatively. The runners appeared to be attracted towards the unshaded area from individuals existing in the surrounds. Runners of *T. repens* were defoliated by the action of treading and were pressed into the puddled ground, but in many cases recuperated.

II. FLAGGED FOOTPATHS.

Several types of flagged pavements are in existence, the commonest being the ordinary street sidewalk. In this case the flags may be of stone or concrete, but in both cases interstices exist between the flags. Garden paths and field paths are sometimes flagged and even asphalt paths possess a curb which is composed of individual stones. Cobbled paths and roadways are now of uncommon occurrence.

Except in the centre of large cities or in the presence of chemical fumes or similar agents destructive to plant life, all flagged pavements possess vegetation, though this is in many cases extremely scanty. Lower forms of plant life such as mosses and algae may cover the flags or exist in the interstices, but their distribution is not considered in this paper.

The complete floristic list of the habitat is indefinitely large and ranges from seedling trees to grasses, but the frequency of the majority is of so low an order as to be negligible. They are accidentals, occurring in odd sheltered or protected places.

The remarkable character of the vegetation of this type of habitat is the predominance of *Poa pratensis* over all other species. This grass occupies the

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interstices between the flags, sometimes dominating this area and sometimes occurring in scattered colonies. It is practically constant for all examples occurring on flagged pavements in the most varied localities. It has been observed as the dominant species of flags and kerbstones for miles along a road crossing Derbyshire moors, on the promenades of seaside resorts, and in the suburbs of cities in all parts of the country. Subdominant species are *Galium* spp. and *Sagina procumbens*.

Where the flagged path borders a bank or wayside the latter situations may be populated by a large variety of species, yet *Poa pratensis* still dominates all the interstices of the flags. In a survey of twenty examples it was found that whereas *P. pratensis* occupied an average area of only 5 per cent. of the vegetation of the surrounds, it composed 95 per cent. of the vegetation of the interstices assessed on an area basis ((2), p. 585).

There appear to be two reasons for the dominance of this species, firstly the ability to invade the interstices by means of its runners, and secondly the adaptation to resist the injury caused by the very severe and concentrated treading. This power of resistance is due to life form and leaf and stem structure and has already been fully described.

In the case of disused flagged paths or those rarely trodden, the flora may be extremely varied and possess no distinct characters; this also applies to cobbled paths. The colonisation of a newly laid flagged path takes place by seed infection of the soil of the interstices and by invasion from the surrounds of runner-bearing species. The commonest ubiquitous annuals may appear together with *Agrostis* or *Agropyrum*. *Poa pratensis* may appear as isolated seedlings in the interstices or from runners invading from the surrounds. The mechanical effect of treading soon exerts its selective influence, *Poa pratensis* surviving on the closely trodden portions.

Pl. XXXVI, phot. 3 shows the domination of an interstice by *Poa pratensis* while the immediate surrounds Pl. XXXVI, phot. 4 contain a mixed flora.

III. CART-TRACKS AND GATEWAYS.

Cart-tracks, frequently used lanes, fen droves and gateways cover a large area of the countryside, probably of greater magnitude than that occupied by footpaths. They are all subjected to the same mechanical influences, i.e. human treading, and in addition the deep disturbance and churning action of horses' hoofs and of cart-wheels during wet weather. In summer the surface may be hard and stable, but in winter certain parts of it will become a morass.

On cart-tracks and fen droves the characteristic species are knotgrass (*Polygonum aviculare*), swinescress (*Senebiera Coronopus*), silverweed (*Potentilla anserina*), greater plantain (*Plantago major*), rayless chamomile (*Matricaria suaveolens*). The grasses are *Poa annua*, *P. pratensis*, *Lolium perenne*, while associated with these there may be *Trifolium repens*. Distinct zonation exists on these areas, and upon examination it is found that the most disturbed



Phot. 3. Surrounds of flagged path. *Agrostis stolonifera*, *Festuca ovina*, *Ranunculus* spp. and *Carex luteoliana*.



Phot. 4. Flagged path, interstices dominated by *Poa pratensis*.

regions are dominated by the annuals, while perennials dominate the more stable regions. The most severely trodden and compressed portion of the stable surface do not, as a rule, support grasses, but the less trodden and compressed part of the stable surface and the margins of the habitat may be dominated by the perennial grasses and by *Trifolium repens*.

This community may usually be defined as an associates. The magnitude of the area and its separation by ditches or hedges from the surrounding communities should entitle it to this rank. It contains consocieties, societies and colonies. It is obviously in an unstable state.

Gateways exhibit a somewhat similar flora and the constancy of the species is the same throughout the country. The obvious reason is that the mechanical factor is again the most potent. The phenomenon of zonation is also observed, especially where a gateway enters a grass field, and this zonation gives an excellent example of specific changes in response to varying intensity of compression. In the actual gateway midway between the posts is an area of bare ground where disturbance and treading are so severe that no species can exist while these continue. Following upon this is a zone in which *Polygonum aviculare* and *Matricaria suaveolens* are dominants. Intermixed with the latter species, but extending further out, *Plantago major* is a constant.

Transient individuals of *Poa annua* may occur over any part of the area at certain seasons, most commonly in winter and spring. In the gateway of a pasture, grasses exhibit a zonation consisting of the same species together with *Trifolium repens* and arranged in the same way as on footpaths. The grass zones are furthest from the gateway and merge into the pasture.

Gateway communities may also be described as associates, being subordinate communities in the midst of cultivated or semi-cultivated vegetation communities.

Quantitative data. In five examples composed of two gateways, two cart-tracks, and one fen drove a survey revealed the following data. The species *Plantago major*, *Polygonum aviculare*, *Matricaria suaveolens*, *Senebiera Coronopus*, *Potentilla anserina*, *Poa pratensis* and *Agrostis stolonifera* were present in all cases with the exception of one gateway where *Potentilla anserina* was absent. The relative abundance, and also the areal percentage occupied varied greatly with each example, for the size of the individual plants was extremely variable. Frequency did not vary to quite the same extent, which was probably due to a certain amount of zonation of the species. The fact that the above species were the co-dominants is revealed by the fact that other species, grouped as miscellaneous, only showed an average abundance of 3.6 per cent. of the total.

In a hundred examples the following percentage constancy of the species was recorded: *Plantago major* 100, *Polygonum aviculare* 92, *Matricaria suaveolens* 89, *Senebiera Coronopus* 79, *Potentilla anserina* 60. *Poa pratensis* 94, *Agrostis stolonifera* 54. One or more other species occurred in all the examples.

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Qualitative data. No species could be described as exclusive to the community, but the first five in the above list could be classed as preferential.

As regards vitality, miscellaneous species were accidental and did not multiply. *Agrostis stolonifera*, originating from adjoining situations on stable ground, showed restricted vegetative development. The remaining species of the community regularly completed their life cycle.

The periodicity of the species varied, in that *Poa pratensis* was winter green while the other species were dormant (or absent in the case of therophytes) in the winter aspect. *Polygonum aviculare* and *Matricaria suaveolens* do not appear as seedlings until late in the spring aspect.

The distribution within the community, apart from the phenomena of zonation, showed one outstanding feature, i.e. that perennials do not exist upon the areas which have been disturbed and puddled in winter, except in a seedling or "maiden" state. These areas are dominated by the annuals *Matricaria suaveolens* and *Polygonum aviculare* and in some cases by seedlings and immature plants of *Plantago major*.

Habitat factors.

The habitat of the community under consideration bears some features of resemblance to that of the footpath, in that it is a disturbed area, and the disturbance is due to puddling. In this case, however, the disturbance is of a much more violent nature, the soil being puddled and disturbed to depths of several inches, or in the case of cart-ruts even to the depths of the axles. Certain parts of the area are disturbed during winter months when the ground is soft, other parts, as, for example, the region between the cart-wheels and the horse's hoofs, remain undisturbed. During summer the ground becomes hard, and though still subjected to pressure, comparatively or quite stable.

Edaphic factors.

Since the gateway and footpath communities are constant for all types of soil, the chemical composition of the soil and to a certain extent its physical condition, i.e. humus, clay, sand or chalk content, cannot have any definite influence upon the flora. On sandy heaths (Bawsey and Snettisham, Norfolk, Greensand formation) the same flora is found as upon heavy clays. On soils containing a clay fraction "poaching" and deflocculation of the clay particles occurs, but this is not the case on sands.

Light.

Owing to the absence of other vegetation the habitat is fully illuminated, as was the footpath. There appears to be some connection between the light factor and the vegetation, as all the species except *Matricaria suaveolens* are prostrate or straggling, and unable to compete for light in other habitats. *Matricaria suaveolens* is a Composite with dissected leaves, and it is well known that species of that family and with that type of foliage are extremely intolerant of shade.



Phot. 5. Fen drove, aestival autumnal aspect. *Polygonum aviculare* is dominant between the tracks.



Phot. 6. Fen drove with *Potentilla anserina* and *Plantago major* dominating the undisturbed region between the cart-tracks.

BATES—VEGETATION OF FOOTPATHS, SIDEWALKS, CART-TRACKS
AND GATEWAYS

In the above connection observations were made in several localities on the reaction of *Matricaria suaveolens* to light. The first three were cart-roads running east and west. When the hedge was dense or the ground overshadowed by it or by trees, *Matricaria suaveolens* was absent or scanty. In one example, at Castle Rising, Norfolk, a building shaded the sidewalk up to the inner edge of the kerb. A little *Matricaria suaveolens* grew under the wall and on the sidewalk, but it was abundant upon the kerb.

It is a significant fact that *Matricaria suaveolens*, *Senebiera Coronopus* and *Polygonum aviculare*, all germinate comparatively late when most places are overshadowed by vegetation. Seedlings of these species are not to be observed on cart-tracks or in gateways until the end of May. It is highly probable that these are the only habitats offering light and a suitable situation for germination at this season.

Thus it appears that light is a contributing factor to the existence of the cart-track and gateway community.

Disturbance and compression.

It is obvious that the chief factor influencing the habitat is that of disturbance of the ground during winter and compression of the surface in summer when the ground is dry. The effect of the winter disturbance is to destroy all species which have become established during summer. These species consist of the annuals *Polygonum aviculare*, *Matricaria suaveolens*, *Senebiera Coronopus*, and the seedlings and first year plants of *Plantago major*, together with a few miscellaneous seedling perennials. The annuals would obviously die irrespective of the disturbance, but the perennials are also destroyed. Observation shows that runner-bearing perennials are crushed beneath the wet soil, while *Plantago major* is squeezed out and left upon the surface to be destroyed by frost or other agencies. In any of these communities the perennials of more than one year's standing are found on parts of the habitat which are stable during winter.

Potentilla anserina, having its main rootstocks established upon stable undisturbed ground, may during summer send runners over an area which was disturbed during winter. It does not, however, tolerate much treading.

Pl. XXXVII, phot. 5, shows the aestival-autumnal aspect of a fen drove; the surface is colonised by *Polygonum aviculare*; in winter it was a morass devoid of vegetation. Pl. XXXVII, phot. 6 shows *Potentilla anserina* and *Plantago major* dominating an undisturbed region between cart-tracks.

The structural resistance to treading.

Plantago major, *Matricaria suaveolens*, *Polygonum aviculare*, *Senebiera Coronopus* and *Poa pratensis* are all resistant to treading. The resistance of *Poa pratensis* and *Plantago major* in virtue of their life form and structure has already been discussed (p. 477). The remaining species are also adapted to this influence.

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Polygonum aviculare has hard wiry stems which resist treading, and the prostrate form prevents snapping of the stem at any given point. The leaves are small and become much smaller when the plant is subjected to treading. The flowers are minute and are protected in the axils of the leaves. *Senebiera Coronopus* is prostrate, has small scale-like leaves and small flowers and thus survives compression. *Matricaria suaveolens* is normally an upright plant but can become prostrate. The ability of this species to resist treading appears to be due to the small area of finely dissected leaves, and the extremely pliable nature of the stem, which is tough and fibrous and does not snap if bent double. The flower heads are comparatively large, but if compressed they splay out and appear to escape injury.

It must be made clear that the species of the community do not flourish under compression, but are severely stunted in growth both with regard to the shoot and the root system. They are also altered in habit, being converted from the upright or semi-upright to the prostrate habit. In spite of this severe stunting they are, however, capable of completing their life cycle.

GENERAL SUMMARY.

I. The chief factor concerned in the production of the footpath socies from the grassland community is the mechanical effect of treading and puddling. This exerts a selective influence on the grasses, eliminating those not structurally adapted to withstand the injury of treading and puddling. The species adapted by virtue of life form and leaf and stem structure are able to persist. These dominants are zoned according to the intensity of treading. Under dry conditions where no puddling occurs, treading alone produces little change.

The plantains are governed by the same factor as the grasses and owe their existence to their life form. *Trifolium repens* does not exhibit as great a resistance to treading as do the grasses and hence occupies only the outer zone of the footpath. Light appears to be a decisive factor with this species, shading being eliminated by the treading down of taller species.

II. The interstices of flagged paths and sidewalks are dominated by *Poa pratensis*. This is because this species can invade the area by means of runners coupled with its structural adaptations to resist injury by treading.

III. The characteristic flora of a cart-track or gateway community, owes its existence to a peculiar combination of circumstances. Severe disturbance and churning of the ground in winter exterminates all perennial species which have seeded during summer, annuals dying naturally or as a result of this disturbance. During summer the disturbed area becomes hard and stable, but is still subjected to surface pressure, and is therefore populated by annuals or by seedling perennials (chiefly *Plantago major* and *Poa pratensis*). In virtue of their life form and habit, these are able to resist the injury of treading to a sufficient degree to continue their existence through the summer and autumn. Other species than the above may appear during spring and summer as acci-

dentals, but succumb to treading. The undisturbed areas between or around the disturbed region are populated by perennials which may resist a severe degree of treading, but cannot survive disturbance and churning of the ground during winter.

All the species are ill adapted to compete for light and the habitat offers illumination without competition. It also favours species which germinate comparatively late in spring.

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SUCCESSION, DEVELOPMENT, THE CLIMAX, AND THE COMPLEX ORGANISM: AN ANALYSIS OF CONCEPTS

PART III. THE COMPLEX ORGANISM: CONCLUSIONS¹

By JOHN PHILLIPS.

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THE COMPLEX ORGANISM AND THE BIOTIC COMMUNITY.

I HAVE hinted in several places in this paper that I believe a thoroughly natural and dynamic treatment of succession, development and the climax to find its basis in the concept of the complex organism—the organism represented not by vegetation alone but by the *biotic community* wherein plants and animals are intimately integrated associates. For this reason, I include a brief treatment

¹ It may be thought that much of the subject matter of this article is unsuitable for an ecological journal since it deals with philosophical topics. The decision to publish it *in extenso* was taken because it "rounds off" Prof. Phillips' theory of vegetation and will thus assist readers to comprehend his position—ED.

of the biotic community in this section dealing with the complex organism and two intimately related concepts: emergent evolution and holism. For the sake of clarity, I discuss the principal features in this difficult and highly polemical field under appropriate heads and subheads.

THE COMPLEX ORGANISM.

Historical summary: emergence, holism, complex organism.

No treatment of the concept of the complex organism would be satisfactory without reference to the concept of emergence or emergent evolution and holism, as well as to the views of organicist philosophers and biologists. Indeed the contributions—based upon the most diverse experiences and materials—made by philosophers, sociologists, biologists concerned with the simple or individual organism, students of evolution, and ecologists interested in the nature and relations of communities, have not only produced an ever-increasing volume of as yet unorganised information awaiting integration, but also point a warning finger at the extreme specialisation that has permitted the investigation with almost complete absence of co-operation of this fundamentally important border-line field of science and philosophy. Without collaboration among students of various shades of experience, and possessing minds capable of critical discrimination and synthesis, a really satisfactory synoptic survey of fancies, facts and theories is impossible. Within a certain region of this field General Smuts (1926) has attempted a synthetic survey. This region however is insufficient for our general purpose, and it must also be remembered that since the publication of *Holism and Evolution*, students of synecology have assembled information hitherto unavailable, or very largely unavailable, to the author of that epoch-making book. It must be emphasised, of course, that even with the yearly increased provision of facts, and of knowledge concerning the meaning and interrelations of such facts, it must be long before we have sufficient ecological knowledge assembled to satisfy ourselves. In the meantime it may interest and inspire ecologists studying appropriate aspects in synecology to know that General Smuts' need for refinement and for extension of his theme is more and ever more facts, interrelated facts, suggestions and soundly based ideas regarding organisms, communities and the changing stage—the habitat—on which they play their part.

For the sake of bringing together some of the more important references in the history of the concepts under discussion, I give below historical summaries that will more than justify their existence should they lead to a better acquaintance, on the part of ecologists, with the writings of the students cited.

(1) *Emergence or emergent evolution.*

Very briefly and generally stated, it is the view of the authors and disciples of this concept that there is a creative synthesis and emergence of properties, structures, forms, stages or levels; such newness, springing from the interaction,

interrelation, integration and organisation of qualities—whether these be inorganic, organic, or psychic—could not be predicted from the *sum* of the particular qualities or kinds of qualities concerned; integration of the qualities thus results in the development of a whole different from, unpredictable from, their mere summation. Particular stress is being placed upon the emergence of the new—this especially being so in the instance of one of the concept's most brilliant protagonists, Lloyd Morgan (1923).

Quot homines tot sententiae is as applicable to this concept as anywhere else in the field of human knowledge, hence it is scarcely necessary to record that there are in the literature various modifications of the above definition. As the emphasis is laid upon the development and appearance of emergents, it is plain that the concept, while applied by some philosophers in a cosmic sense and by others to a restricted sphere such as the psychic, has interest to the sociologist and to the ecologist. For the ecologist it appears to offer a vantage point from which to survey characteristics of novelty, of integration, of wholeness, emergent from succession and development in biotic communities. Direct contact is thus seen to be possible, nay, essential, with the thesis that communities are not mere summations of individual organisms, but are integrated wholes with particular emergents. As may be seen from my summary of holism below, there is a distinct point of contact, here, with the concept of General Smuts, despite the fact that holism demands yet something more: the character of wholeness as an active cause.

Wheeler (1928), the notable student of social phenomena among the insects, has recently given an interesting account of emergent evolution in relation to the development of societies; he includes numerous historical references, and from some of these I have drawn. That the organism was different from the sum of its parts appears to have been suspected by the vitalist Stahl (1660–1734) and the two mechanists Reil (1759–1813) and Rudolphi (1771–1832), while J. S. Mill (1843) deals with the concept under his discussion of “heteropathic laws” in causation. The eminent physiologists Du Bois-Reymond (1848)—in his study of animal electricity—and Bernard (1865) make reference to it, Bernard, for example, giving the now classic example of the properties of oxygen and hydrogen not accounting for the properties of water.

Lewes (1875) suggested the term *emergent* for any novelty emerging: this being in contradistinction to *resultant* or mere summation. Early in the new century the famous psychologist Wundt (1903) gave his support—his term for emergents being *creative resultants*—and as regards psychologists, it is not without interest to note that the famous Wertheimer-Koffka-Köhler, or Berlin, School of “Gestalt” psychologists were in agreement, and that recently Wheeler (1928, pp. 33, 36) has been able to discuss as true *Gestalten* certain structures and activities in social insects such as ants and bees. Henderson (1917) terms emergence *organicism*. Alexander (1920) is responsible for considerable development of the concept in his work on *Space, Time and Deity*;

Sellars (1922) terms emergence *evolutionary naturalism*; an outstanding contribution is made by Lloyd Morgan (1923); Broad (1925) refers to emergence as *emergent vitalism*. Strong criticism of the habit of most authors in artificially isolating the emergent whole from the habitat, and in failing to remember that the parts of the whole have relations one with the other, is made by Wheeler (1928, p. 21), who considers along with Brown (1926) these errors to have been instrumental in producing abstraction and a sense of mystery. Regarding this tendency to isolate the emergent whole from habitat and from its own parts, Brown argues that the extraordinary sense of mystery some people appear to feel about the process of emergence may arise from forgetting this setting, which is as real as the selected elements studied; such omission makes technically false the literal interpretation of the appealing paradox that the whole is something more than the sum of its parts.

Disagreement with the concept is expressed by Russell, Morris and Mackenzie (1926), to which Lovejoy (1927) makes vigorous reply commended by Wheeler (1928, p. 69). A staunch apostle among biologists is found in the notable zoologist Jennings (1927, p. 20; 1933, p. 30), who ably contends that new things, new methods of action following new laws, which are not computable, appear as evolution progresses and that concretely the concept includes the thesis that such new things and new modes of action distinguish the living from the non-living, the social from the solitary. Among sociologists, Sumner and Keller (1927, p. 2220) warmly advocate the principle of emergence, saying, for example, that from sulphur, charcoal and saltpetre it would be impossible to predict the characteristics of gunpowder, that it is impossible to juxtapose cells and judge what they will make, and that the juxtaposition of human qualities in human society does not guarantee the quality of a society. Their support is somewhat difficult to understand in the light of their marked opposition (Sumner and Keller, 1927, p. 2182) to the belief that the organicist or organism concept has any utility in the study of society, a point referred to under the next subhead. Among other supporters of the concept may be mentioned Holt (1914), Gordon (1926), Ogden (1926) and Parker (1926).

Lloyd Morgan (1923, p. 4) suggests that Browning in *Abt Vogler* poetically lays stress in the word "star" on the *emergent* character of "chordiness"—something more than the additive resultant of constituent tones: "And I know not if, save in this, such gift be allowed to man, That out of three sounds he frame, not a fourth sound, but a star."

(2) *Holism*.

Holism is "the fundamental factor operative towards the creation of wholes in the Universe", and is conceived as the basic principle underlying the universal tendency to synthesis: the principle responsible for the origin and development of *wholes*. While it is true that aspects of the synoptic philosophy of Plato and of the views of certain of the emergent evolutionists border upon

holism, it is equally true that General Smuts (1926), in his often reiterated insistence upon the fundamental character of wholeness and the tendency to ever more intensive and effective wholes as the real factor from which creativeness or emergence flow, has introduced a thought, a principle, definitely original and dynamic.

The essential difference between the concept of holism and that of emergence resides, as Smuts (1926, p. 321) himself has stated, in where the emphasis is placed: in *emergence* upon the *emergents*, in *holism* upon the factor operative towards the creation of *wholes*. Hoernle (1926) aptly analyses the difference thus: emergent evolutionists like Alexander (1920) and Lloyd Morgan (1923) have thought in terms not of wholes but stages; others like J. Ward have conceived wholes, but spiritual wholes only. He rightly refers to Boodin's (1925) related concepts of empirical realism and cosmic idealism as inviting comparison with Smuts' concept (a study of Boodin, however, reveals many important differences), and prophesies that holism—if scientists are willing to receive it—will mean a re-orientation of scientific thought. He is being proved right in the instances of those few ecologists who so far have attempted to apply it in their investigations of biotic communities. Holism as the operative cause and emergents as portions of its fruits are inherent, dynamic characteristics in communities; they originate, develop and integrate from field to field, from level to level, as biotic development progresses from pioneer communities to those that are in dynamic equilibrium with a dynamic habitat. Any but a static view of the structure, composition, and life of communities must admit not only the interesting bearing of the concept of holism upon the study of dynamic community ecology, but cannot fail to be impressed with the fundamental nature of the *factor of holism* innate in the very being of the community, a factor of *cause*. I deal briefly with the whole as a cause under a subhead in the sequel.

Haldane (1928, p. 136), while unable to agree with all the aspects of Smuts' concept, points out the great advance made by it: in the substitution of an intelligible conception of a *wholeness* for an unintelligible *élan vital*. Hogben (1930, p. 291) concludes that holism contains within it no promise of future progress, while Worrall (1933, p. 141) dismisses it as quite evidently a supernatural invention—a fantastic fiction.

For the solution of problems in community ecology at least, I personally find it to contain promise of much that otherwise would for ever remain obscure, and I certainly am able to perceive its grand utility for life as a whole; so far from being a fiction it has become to me the deepest and most abiding reality, paradoxically both a starting point and a goal in the scientific study of communities. I have hinted elsewhere (Phillips, 1931*a*, 1932) the utility of the concept in ecology, more especially in connection with the complex organism—the biotic community.

(3) *The complex organism.*

Since the time of the positivist philosopher Comte (1832) at least, there has been a belief in certain circles that communities—and the principal emphasis has been upon human communities—possess characteristics of *mass* or *complex organisms*. In the light of the far-reaching importance of this concept in the study of succession, development and the climax, it is of interest to note the names of a few of the more important holders of this point of view.

It should be mentioned, however, that definition of *organism* (in the “social philosophical” sense) is variable; Needham (1928, pp. 80–1) has drawn attention to this, and gives as examples of diversity the concepts of organism held by such workers as Lloyd Morgan (1923), Whitehead (1925) and C. D. Murray (1926).

Spencer (1871) is a keen protagonist of the social organism, as is L. F. Ward (1894, 1903). As Wheeler (1928, p. 59) says, it is somewhat remarkable that while Spencer and Ward both believed in *emergence*—Ward’s term being *creative synthesis*—neither of them attempted to apply the emergence concept to social organisms. Pareto (1917) is another supporter.

Wheeler cites Ferrière (1915), Bristol (1915) and Barth (1922) as being in marked opposition to Spencer, von Lilienfeld and others, in regard to their concepts of the social organism; he contends that these critics themselves show but a superficial knowledge of animal sociology, and altogether fail to observe the striking analogies existing between individual and complex organisms. Hogben (1933, p. 9) points out that the basic problem of social evolution in *human* communities primarily concerns the generation of new modes of behaviour in a rapidly changing man-made habitat: in this respect human society has no precise parallel among other social organisms. With this I cannot agree: man reacts upon his habitat most assuredly; but so do all plants and all animals—otherwise the whole of our concepts of succession, development and the climax in dynamic equilibrium would be fantasy!

An amazing attitude—in the light of their already mentioned acceptance of the doctrine of emergence—is adopted by the notable students of human sociology, Sumner and Keller (1927, p. 2182), who contest the concept of society as an organism: if 1000 persons, selected by chance, were questioned on this matter, in the absence of a “logician” or “word-juggler”, the authors contend that the answer would be against the concept; this and other examples they use in their argument against the scientific utility of analogy.

So far there has been no record of the concept being applied to communities in which plants play either the major role or one equal to that acted by animals. It remained for Clements (1901, 1904, 1905, 1907, 1916, 1917, 1920, 1917–33) to hint at, to apply tentatively, to develop and to use as a fundamental basis the conception that plant (later biotic) communities function as complex organisms, his use of the adjective being based upon his desire to differentiate clearly the individual organism from the mass organism. At first given little or no atten-

tion, for a season somewhat derided, for another treated with condescension by most ecologists, this concept is gradually being accepted by a few, has gradually met with ever-increasing respect from a larger number of others. Further details are given under the appropriate subheads following.

From the foregoing summaries of the three concepts—emergence, holism and the complex organism—it should be plain that they are inherently inter-related: holism the causal factor: emergence arising from this factor: the complex organism an integration of emergents, of wholes of potential development, to yet a more efficient whole. I examine below the views of certain workers regarding the complex organism.

Various theses.

Thesis: There is no complex organism represented by plant or biotic communities.

Gleason (1917, pp. 464–5; 1926; 1927; 1929, p. 643), as might be expected from his attitude towards succession, development and the climax, is strongly opposed to the view, and stresses, on the contrary, that the phenomena of “vegetation” depend completely upon the phenomena of the *individual*; any analogies drawn between an organism and a unit of vegetation are always more apparent than real, and never rise to the rank of homologies. An apt reply is made by Tansley (1920, p. 126) to the effect that Gleason’s reasons against the unit of vegetation being an organic entity are not convincing, that obviously the phenomena of vegetation depend completely upon those of the individual but that this statement applies equally to the human community which everyone would agree must be considered an organic entity: units of vegetation possess *some* of the characters of organisms.

Tansley’s remarks upon the *human* community are especially interesting in the light of the already mentioned disagreement on this point by Sumner and Keller (1927, p. 2182); Tansley’s (1922, p. 245) further views upon human communities not escaping from the implacable determinism governing plant communities, and equally upon plant communities as *quasi-organisms*, are well worth reading with reference to the claim of Sumner and Keller.¹

As regards plant communities, Gams (1918), Lüdi (1919, p. 55) and Du Rietz (1919; 1921, p. 98) among continental ecologists, vigorously disagree with the concept; Cooper (1926, pp. 394–6, 399–401) expresses himself as in very marked disagreement, and holds that Clements’ (1916, p. 3) use of the concept as a basic tenet in successional and developmental studies detracts seriously from the usefulness of his contribution to these subjects. His remark that acceptance of the concept colours the whole of his treatment of succession and development is, of course, true.

A supporter of Clements as regards the monocl意思 theory, Braun-Blanquet (1932, p. 315) refers to Clements’ comparison of the climax com-

¹ It is interesting to note that Toynbee (1934) in his monumental work on the history of civilisations, regards these as entities, which are born, may develop, and die.

munity to an organism showing birth, growth, maturity and death, as "a flight of imagination".

Thesis: The plant or biotic community shows characteristics of an organism up to a particular point: there is analogy between the individual organism and the community—in certain respects.

Up to a point it is considered by some legitimate and helpful to compare phenomena in the life of the community with phenomena in the life of the individual organism, but it is urged that the community is not an organism in the full sense in which the term is applied to the individual organism serving to build it. Organic entity, at any rate, is admitted, even if the full comparison with an organism be rejected. Utility of the proposition that analogy exists between phenomena of the individual and those of the community is conceded as being evident for purposes of a natural classification of communities, since it certainly involves what Tansley (1920, p. 126) terms the *characteristic relationships* of the vegetation units to their habitat and to one another.

Moss (1913, p. 21) seems to have been among the first of the British ecologists to formulate the view that a plant formation has a life history: it is born, it enters on a period of infancy and adolescence, it attains maturity, it becomes senile, it decays: but throughout these stages, it is the same organism, characterised by a definite habitat related to a correspondingly definite flora. Among students of animal communities, S. A. Forbes (1887), in his classic paper "The lake as a microcosm", concludes that a group or association of animals or plants is like a single organism, in that it brings to bear upon the outer world only the surplus of forces remaining after all conflicts interior to itself have been adjusted: a remarkably advanced view to have expressed in his day and generation! We are indebted to Tansley (1920, pp. 122–3, 126; 1929, p. 678) for several fair and balanced discussions. Tansley is prepared to accept the concept up to a point, the point where useful analogy with the individual no longer holds; he is further agreeable to its use provided it is applied to his *autogenic* succession (succession due to biotic reaction) only. This last limitation is indeed no limitation at all to Clements and his associates and myself (Phillips, 1934, p. 565), for we acknowledge no process as succession unless it be due to biotic reactions. Furthermore, he suggests the term *quasi-organism* (1920, p. 126; 1929, p. 678) probably because he thinks it more suitable etymologically. He argues (1920, p. 122) that because communities may usefully be treated as organic entities, or because they may be compared up to a point with organisms, it does not follow that they *are* organisms. With this general view Fuller (1918, p. 386) is in accord to a certain extent; he argues that the relationship should be considered as one of close analogy rather than homology.

While the comparison of the community to an organism, even as a simile, cannot be applied indiscriminately to all types of communities, in the view of

Nichols (1929, p. 638), he believes (1923, p. 14; 1929, *loc. cit.*) that the community may be looked upon as an organic entity. To primitive communities, where various individuals exist in virtual independence of one another, drawn together solely by the peculiarities of the habitat, the comparison of an organism cannot logically be applied. He concludes (1929, *loc. cit.*) that the difference that Tansley (1920) points out as existing between succession and development is essentially the same sort as that existing between the association (community) considered as an entity, and the association compared with an organism.

Yapp (1922, p. 11) regarded the organisms occupying any given habitat as woven into a complex, but unstable web of life, and his sympathy with Vestal's (1913, p. 13) concept of "single biotic associations" leads me to regard him as partially in support of the thesis under consideration.

So far as insect societies are concerned Lameere (1920, p. 513) is impressed with the utility of considering them as analogous with individual organisms.

Thesis: The plant or biotic community behaves as, and actually is, an integrated whole: a complex organism, which exhibits various life phenomena in a manner similar to an individual organism: this forms a natural foundation for the study and classification of succession and development in biotic communities.

The community is born, grows, matures, reproduces, and carries out various other biotic phenomena: it behaves in a manner similar to an individual, with obvious and natural differences inherent in its wholly divergent and far more complex structure, constitution and functions. It behaves in such a way as to justify the view that not only is it similar to an organism, but that it is a kind of organism—albeit a highly complex one with idiosyncrasies inherent in its very complexity. On the same basis that it is agreed that the multicellular individual organism possesses characteristics, and the ability of carrying on certain vital phenomena, absent from and impossible in its constituent cells, tissues, organs, unless they be assembled in integrated, organised association, so it is argued that the multi-individual organism, or complex organism, possesses comparable characteristics and abilities not possessed by the individual organism. At different stages, or, to use a philosophical term, within different *fields*, there arise new properties, qualities, or *emergents* definitely unpredictable from a knowledge of the individual organisms and their individual functions, emergents that may be due either to some creative, synthesising factor such as holism, or to profoundly complex and highly effective integration of biotic responses and habitat actions, or both.

Responsible for the original application of the concept of the complex organism to vegetation—and later to biotic communities—and for development of the concept to serve as an efficient, natural basis for interpretation and classification of succession, development and the *climax*, Clements (1901;

1904; 1905; 1907, p. 219; 1909, p. 50; 1916, pp. 3-124, etc.; 1918, p. 372; 1919, p. 336; 1920, p. 327; 1929, p. 202; 1930, pp. 239-40; 1931, pp. 266-8), as has been described in the historical summary to this section, before his views received any but the most lukewarm welcome, met with considerable criticism. I have already referred to the interesting fact that the philosophers were actively theorising about emergents without their being aware that an ecologist and more especially a plant ecologist, quite independently, and on the basis of long-continued observation and intimate acquaintance with nature, was arriving at similar but much fuller conclusions. Clements (1931, in manuscript) truly says that if his critics had been present at the emergence of the first metazoan or metaphyte from its single-celled ancestors, they would have denied that it was an organism at all, because it was different! This is echoed, in part, by Boodin (1925, p. 202), who believes that the step from the unicellular to the multicellular organism is no greater than that from the multicellular organism to the social organism: society is a new level, a new creative adaptation; it is not an aggregate of multicellular organisms, any more than multicellular organisms are aggregations of unicellular ones. Boodin (1925, p. 203), however, points out different "levels" in society, arguing that if nature has experimented a long while in making the multicellular organism so has she experimented a long time in making society. Thus animals living in colonies (the honey bee) and packs (the wolf) he does not consider social groups, but super-organisms constructed upon a plan rooted in organic structure.

Weaver and Clements (1929, p. 314) give the concept support, while among the animal ecologists Shelford (1931, pp. 456-8, 461) and Allee (1931, p. 81) are in agreement. Shelford—who incidentally is a firm believer in *biotic* as opposed to either *plant* or *animal* communities—is particularly vigorous in his comparison of the *biome* (plant-animal formation) with an amoeboid organism, a unit of parts, growing, moving, manifesting internal processes which may be likened to metabolism, locomotion, etc., in an organism. It is clear that the biome differs from the amoeboid organism in having several kinds of "endoplasm", the biotic associations; the *seral* stages are comparable with "ectoplasm". Allee indicates that as an animal may be regarded as a physiological system of physico-chemical processes in dynamic equilibrium, he inclines to define an ecological "animal community" as a system of organisms which is in dynamic equilibrium.

I have recorded (Phillips, 1931; 1931*a*, p. 20) elsewhere that I at one time looked, with General Smuts (1926, pp. 339-43), upon groups, societies, nations and Nature as *organic without being organisms*, and applied this, too, to biotic communities. Since then (Phillips, 1932, p. 16; 1934, p. 566) I have definitely gone further: I have accepted the biotic community as a complex organism, thus agreeing entirely with the concept of Clements.

Furthermore, while (*loc. cit.* 1931) formerly accepting biotic communities as holistic without their being wholes—thus agreeing that these fell into the same

category as General Smuts' (1926, p. 340) groups, societies, nations and Nature—I now incline to believe that these communities are in the nature of wholes of varying stage and efficiency. Smuts (1926, pp. 98–9) himself, in another connection, agrees that “wholes of various grades are the real units of Nature”. As wholes of various grades I conceive biotic communities of various seral stages.

Holism and the complex organism: the whole as a cause.

I desire briefly to outline some features I hold to be of very real importance in the life of the complex organism, the biotic community: features concerning the whole as a cause in development, and in the attaining and maintaining of dynamic equilibrium. During the period in which I was giving thought to this somewhat involved and little explored line of philosophical ecology, I was fortunate enough to hear, as a spontaneous remark, from General Smuts that he considered the most needed material for the development of his concept of holism was that obtainable from the realms of inorganic and organic nature, regarding the whole as a cause. This, I confess, has emboldened me to summarise certain features pertaining to this subject, drawn from contemplation of the complex organism. I submit these in the hope that they may call for criticism. While considerable stress is laid upon the operative importance of the whole, it is salutary to bear in mind the advice of Collingwood (1924, p. 300): we must conceive the part as performing a function in the whole, without which the whole simply would not exist. Wheeler (1928, p. 39), in respect of social emergents, concludes that we are bound to assume that the organisation within the whole is entirely the work of the parts themselves; we should not invoke *entelechies* (Driesch, 1908) *organisatory factors* (Eldridge, 1928) or *élan vital* (Bergson, 1911).

The subject is treated below in summary fashion; further details must await special treatment in a subsequent paper.

(1) At different levels the whole reacts upon habitat, changing (ameliorating) this for higher level wholes; the reaction of a whole, taken into account with its particular habitat and with the interrelations existing among its constituent organisms, shows as emergents, changes in the habitat that are different from the sum of the changes that the constituent organisms would undergo were these not in communal association. I realise, fully, that this statement calls for the logicians' taunt: “More out of less... Something out of nothing. Verily a miracle; the stream rising beyond its source” (Hoernle, 1932, pp. 164–5). Without forgetting Brown's (1926) warning regarding the importance of taking into account the interstitial filling of habitat and interrelations existing among the parts, I submit that the accumulation of ecological evidence is becoming so impressive that I am not seriously perturbed by the strictures of formal logic.

(2) The whole at different levels provides floristic-faunistic structural,

developmental reaction, competition, co-operation, and evolutionary-potential features. In wholes at closely related levels, these features are in some instances identical, in others similar, in others distinctly new; in wholes of widely diverse level, the features are more frequently distinct, a few common features of course remaining: as indeed they do in the individual organism. In other words, the whole is the cause of new features within the complex organism: because the whole, at a level preceding, brings about conditions congenial to the constitution of the whole at the level succeeding.

(3) It has been stated under "Conclusions regarding the climax" that the climax stage should be conceived as being in dynamic equilibrium with its habitat. The climax stage whole, in order to be in temporary equilibrium with the habitat, which lower level wholes and the climax whole itself have moulded, is in a continuous state of adjustment: it regulates here, undergoes temporary change there, begins, continues, completes series of microcosmic successions and stages of development.

Its very existence, its very wholeness, are causes of this adjustment. At lower levels, the stages are less nicely balanced with the habitat; the degree of adjustment is much less delicate; gross changes often take place more rapidly than do minute changes within the climax whole. Delicacy of adjustment then, is an emergent from the existence of the climax whole. Competition and co-operation balances are more finely struck; the *action-co-action-reaction* chain of cause and effect is closer linked, more sensitive to stimulus in degree and kind.

As regards the mutual relations of the parts in the whole, and of the whole itself to the habitat, Woodger (1929, p. 451) has pointed out that in the individual organism, too, this continues to persist in spite of alteration in the habitat, by means of a change in itself.

(4) Integration is more efficient in a higher stage whole than in a lower, finding its quintessence of efficiency in the climax whole; such integration concerns the biotic interrelations as well as the relationships existing among presence, size, abundance, efficiency and general activity or influence of the biota and the physical factors of the habitat. The higher the whole, the higher the degree of efficient integration. I must emphasise, however, that this does not automatically imply that a higher whole in the community—or elsewhere in Nature—is necessarily more complex or complicated than a lower; efficiency is often associated, not with complexity, but with a greater simplicity.

(5) Different stages in succession and development—i.e. different levels of wholes—provide, as indicated under (2), more or less distinct biotic and physico-chemical conditions for production of variation in function, in form, and thus for evolutionary change. Conceivably, the sequence may be: a factor complex, a biotic array of *specients* (Clements' (1931, p. 267) term to emphasise that each individual possesses a dual nature: as individual and as species or genus: hence the *specient* is the *individual-species*) emergent from a

change in level of the stage, of the whole, producing a variation in function, this variation being the root cause of change in form, this function-and-form change in due course being intensified, being interwoven into the phylogenetic constitution of the organisms concerned. Bews (1927) has suggested that extreme habitats appear to present more effective features for production of change in plants. Logically, this could be interpreted as implying that the more primitive habitats under control of lower level wholes or early seral stages, would be more effective in the evolutionary sense than would more highly developed habitats. We have, however, to take into account not only habitat *levels* but also the levels of organism response and reaction; hence, it behoves us to study carefully the relation between level of whole and degree and quality of evolutionary change.

(6) In the climax whole, the more efficient wholeness causes most marked possibility of reproduction. In the wholes of lower level—the seral stages—reproduction in the sense of continuation of the particular stage is either not possible at all—where one stage follows another with rapidity—or is possible within a limited sense and for a relatively limited time only. In the climax stage reproduction is possible for periods ranging from hundreds to many thousands of years; indeed, until there be an effective change in the general climate of the region.

(7) As the stages of development proceed toward the climax the extent of optimum association, i.e. optimum balance as regards competition and co-operation among the biota, increases. Emergent from the fact of its own greater completeness as a whole is the cognate feature that the quality of optimum association has developed too. Antagonistic co-operation—so aptly defined by Sumner and Keller (1927, p. 2334) in the statement: “politics makes strange bed-fellows”—with increasing stage of wholeness shows a finer and yet finer balance struck between antagonism and co-operation, so that co-operation emerges less and less shackled by antagonism.

Further examples could be given, but sufficient has been said to illustrate my belief that a synthesising, operative factor is at work, call this factor holism or whatever else one will; at all events these examples have to be explained by J. M. Robertson (1926) and other critics of the concept of holism.

THE BIOTIC COMMUNITY.

It is not my intention to enter into a detailed discussion of the concept of the biotic community, as this has been done elsewhere (Phillips, 1931*a*). I desire, rather, to correct several errors in citation made in my earlier paper, to include several references to important contributions made since the reading of that paper in August 1930, and to emphasise the need for restriction of the term biotic community to naturally associated organisms.

*Corrections in citations given in this JOURN. 19, No. 1, pp. 1-24,
"The Biotic Community".*

As regards the development of the concept that plants and animals are interrelated, co-acting constituents of an integrated biotic community, I am able, through the aid of information given me by Dr Clements, to record that the historical sequence was for American workers, at least, as follows: The first suggestion of identity between many plant communities and animal communities was made by Clements (1905). This was followed by Vestal's (1913) suggestion of "single biotic associations", and by Clements' (1916*a*) concept of the biotic formation or *biome*, developed by him further in *Plant Succession* (1916). It was not until Clements in 1918 proposed a co-operative project in grazing research—a subject in which emphasis must be laid as much upon animals as upon plants—that W. P. Taylor and Vorhies became the first zoological converts; Shelford a few years later accepted the concept on his own initiative, and in 1924 stated publicly that progress in animal ecology depended upon employing the concepts of plant ecology. Among all the students of animal ecology, Shelford deserves principal credit for having reached this conclusion independently. Smith (1928), Shackleford (1929) and Bird (1930) were the first to attempt to put into practice the more detailed concepts and terms of the Clements-Shelford school in the same way that Weese (1924) and Blake (1926) did for the more general ones.

In connection with the naming of communities, with animals in their appropriate role, Taylor was the first to insist that an animal *predominant* be represented in the name; a procedure later adopted by Shelford; Clements objects to this on the grounds of the much more intimate response of plants to climate and their much more basic and universal reaction upon the habitat—the result being their constitution of the real pattern of the climax. Moreover, considerable difficulty is found in selecting the most appropriate animal name, and it must not be forgotten that the plant designation has the additional value of providing for the migratory species of animal, and of those that move from one climax to another.

I desire to record that I should not have included Watt (1919, 1923) among those who looked upon animals as external biotic factors with reference to the plant community; Dr Watt reminds me that in the papers cited he was dealing with specific instances, requiring the particular treatment he gave them; actually, he assures me, he is a keen supporter of the concept of the biotic community.

As regards my citation of Osborn (1929), as a supporter of the view that the animal is an external biotic factor, I am happy to say that Prof. Osborn informs me that he differentiates between such animals as sheep and rabbits, and indigenous animals, so far as their inter-relations with the plant community are concerned; the former class are adventitious to the community as it has evolved, but admittedly the position is quite different in the instance of the indigenous animals.

Citations not included in "The Biotic Community".

Adams (1908, pp. 2-3; 1908*a*, p. 139; 1920, p. 107) refers to biotic successions, the climax as a biotic equilibrium, and (1920) to biotic associations. Klugh (1923, p. 367), whose paper has a most useful bibliography, looks upon plants as part of the habitat of animals. Vestal (1913; 1914, pp. 414, 444) is responsible for two most important papers additional to the work (1913*a*) cited in my paper under mention; Vestal holds that the internal activities of a community are the sum total of the activities of the plants making up the community: plant and animal assemblages—which are mutually interdependent—are extensive parts of a biotic community. Karzinkin (1927) has given an account of biocenosis and appears to be an adherent of the biotic community concept. My attention has been drawn by Dr A. S. Watt to the definition of a forest given by Bailey and Spoehr (1929, p. vii). In the light of their

reference to plants and animals as mutually interacting organisms affected by, and themselves affecting, the habitat, they appear converts to the same concept. Clements and his associates—principally among zoologists, Shelford and Taylor (1930, p. 239; 1931, p. 275; 1932, p. 215)—have continued observations and experiments supporting the concept; Shelford (1930, p. 255; 1931, pp. 453–5; 1932, pp. 107, 110–11) has published several very important papers dealing with both detailed and general aspects, and strongly favouring the concept. There has been a tendency from the ranks of students of pasture management—the contributions of Davies (1933, p. 8) and of Rowland (1933, pp. 307, 316) serving as examples—to conceive the grazing or browsing animal-plant community relation as a biotic community; I have already referred to the desirability of restricting the term to communities wherein the animals are not under the adventitious control of man. In his admirable little work on the ecology of animals, Elton (1933, pp. 4, 38) admits that in a perfectly true sense, animals and plants are bound together into a complex series of biotic communities; but he holds that in most investigations it is found advantageous to separate plant and animal ecology in practice: a point upon which I can agree with him in part only; difference in methods makes for no special difficulty that cannot usually be overcome on the basis of well-organised team work. Moreau (1934, p. 48), who has carried out some excellent work in the realm of tropical African bird ecology, lists vegetation among *indirect* biotic factors so far as birds are concerned. I have referred in various places to the importance of the concept in general ecology (Phillips, 1930*b*, p. 353; 1931, p. 4, 1931*a*; 1931*c*, p. 474; 1931*d*, p. 634; 1932, p. 16). In connection with the tsetse-fly “problem”, I have elsewhere (Phillips, 1930*a*) mentioned the importance of the biotic community concept; in this connection, the summary of Nash (1933, p. 192) is distinctly of interest, although the author does not specifically mention biotic community relations. Nash records that it has been shown that the key to the proper understanding of the ecology of the “fly” community lies in the factors that influence climate; vegetation, although held to be a secondary factor, yet is vitally important, in that the “fly’s” ability to withstand climate hinges upon the presence of a suitable vegetation community; man cannot alter the climate, but he can attempt to alter the vegetation type that enables the “fly to withstand climatic rigours”. Essentially the same general conclusion was arrived at by me (Phillips, 1929, 1930) from a different angle. Allee (1930, 1931, 1932, 1934) continues to be a strong supporter of the biotic community view. It is interesting to observe, however, that a notable entomologist keenly interested in the ecology of insects, Royal Chapman (1931), treats plants largely as a part of the habitat of animals rather than as associated organisms in a biotic community. Ellsworth Huntingdon, well known for his studies in human ecology, informs me that he agrees that the whole organic complex should be considered as a unit.

From the foregoing it is clear that interest in the concept of the biotic community is on the increase; I am able to testify further to this on account of the number of ecologists, in various parts of the world, who have corresponded with me on the topic. In the light of this, and of the work cited by me in 1931, I cannot agree with Wheeler (1928, p. 25)—unless, of course, he is making reference to study of insects only, which his context inclines me to think he is not—who states that apart from a few investigators such as Espinas (1877), Waxweiler (1906), Petrucci (1906), Deegener (1918), Alverdes (1927), Forel (1921, 1923, 1929) and himself, no one has evinced a keen interest in non-human societies.

Finally, I wish to add to the examples drawn by me (Phillips, 1931*a*, pp. 14–19) from the Great East African Plateau a summary of some remarks written by a former colleague in East Africa, Mr G. W. St Clair-Thompson: . . . Given the dominant plants, elevation and province one could make a very fair guess at the larger animals which one would be certain to find there. Given a fairly complete list of such animals and their approximate relative abundance, one, conversely, could visualise the type of country from which they were being

described. Thus—the Palm-*Balanites-Acacia spirocarpa*-Gall *Acacia* country north of Mbugwe (Tanganyika Territory) consisting of at least two well-defined plant communities, is associated very clearly with what seems to be rather an odd mixture: giraffe-ostrich-Thompson's gazelle-baboon-reedbuck-impalla, with Greater Bustard, and incursions of kongoni from the open . . . and nearer Manyara, of elephant in the rainy season.

Similarly Salanga (main road, Kondoia to Arusha, Tanganyika Territory) conjures up bushbuck-reedbuck-leopard in the subtropical evergreen forest, and giraffe-roan in the *Brachystegia microphylla* running down into the very long grass country associated with it and *Combretum splendens*, *Ormocarpum trichocarpum*, *Derris violacea*, and the species of the alluvial valleys.

Knowing the country to which Thompson refers, more especially the Salanga country, I heartily endorse what he has said. Unrivalled opportunities of studying plant-animal relations exist in such new countries as Tanganyika.

Newcombe (1935, 242; 1935 *a*), on the basis of a study of marine communities, stresses the unity of the marine plant-animal community, and the recognition of "plants and animals as interrelated co-acting constituents of an integrated biotic community." Carpenter (1935, 1935 *a*) supports the concept strongly. In a manuscript (1935 *a*) kindly furnished me by the author, he indicates that he believes "the biotic interaction of organisms forms the basic framework for the presence of all communities." He further considers that the establishment of a system of nomenclature omitting any portion of the community in setting up criteria for community recognition and designation, "is a task but partially completed". Taylor (1935) restates his belief in the biotic community concept.

Co-operation in the biotic community.

Allee (1927, 1931) and I (Phillips, 1932, pp. 17-18) have stressed the importance of bearing in mind that co-operation is as important a phenomenon in the life of the community as competition. Spencer (1893, 1893 *a*, 1894, 1894 *a*) strongly urged the necessity for its recognition; Sumner (1906, p. 17) stresses that competition and co-operation are two forms of life association which alternate through the whole organic and super-organic domains, while Sumner and Keller (1927, pp. 2234-7), in dealing with antagonistic co-operation already mentioned by me, state that this form of co-operation is the strongest and most pervasive form of organisation throughout the whole societal structure. Elton (1929, p. 29) says that although each deer competes with its fellows, it yet co-operates with them to form a more efficient unit—the herd. Trenchant criticism of the blindness of nineteenth-century evolutionists—he might have included sociologists and ecologists too—to the co-operative principle in Nature is made by Fausset (1933, p. 232), who concludes that this absence of appreciation of co-operation by these workers was due "to an innate combativeness in themselves"! While treatment of the principle of co-operation in biotic communities must await a special paper, I have felt it incumbent upon me to refer to its fundamental importance as a subject for our earnest investigations along with our study of competition.

CONCLUSIONS REGARDING THE CONCEPTS OF THE COMPLEX ORGANISM
AND THE BIOTIC COMMUNITY.

A few of the more important conclusions that can be drawn from the foregoing discussion of these two concepts follow:

(1) It is clear that since students of emergent evolution, holism, and the complex organism have arrived at certain conclusions strongly reminiscent of one another, a more satisfactory rate of progress towards a better level of knowledge is likely to be attained if they could be induced to work in collaboration: in these days of rapid and easy transmission of information no insuperable obstacles should be encountered.

(2) The biotic community is an organism: a highly complex one; this concept is fundamental to a natural setting and classification of the profoundly important processes of succession, development, and attaining of dynamic equilibrium. If Jennings (1927, p. 20) is justified in asserting that the doctrine of emergent evolution is the declaration of independence for biology, the notable American man of science—not, by the way, a biologist, who stated when criticism of the complex organism concept was rife that to him it seemed the most far-reaching proposal since Darwin—had some justification for his view. As regards criticism that has appeared and is likely to continue: that the concept of the complex organism has little promise of utility in the practical development of the ecology of communities—we can apply, as Woodger (1929, p. 7) applied to the concept of the individual organism, G. K. Chesterton's remark about Christianity: "It has not been tried and found wanting: it has been found difficult and not tried."

(3) For historical reasons as well as by reason of its expressing sufficiently aptly and succinctly the thought it is desired to convey, the term complex organism should be retained; Clements' use of the adjective is useful in focusing attention upon the fact that the individual organism is not meant.

(4) The whole is an operative factor in the community and in the development of one stage of a community to another. This concept is intimately associated with that of the complex organism. Like the general concept of "organism", these two concepts are receiving recognition from physiology, from philosophical evolutionists like Alexander, Whitehead, Lloyd Morgan, and Smuts, from the Gestalt psychologists, and very definitely from some ecologists such as Clements, Wheeler and myself.

(5) Inextricably interrelated with the concept of the complex organism is that of the biotic community. Not only is this community no abstraction, but it is of distinct service in the practice of ecological investigation of the community in its various phases.

(6) Co-operation in its "pure" form as well as in the form of antagonistic co-operation, as a vital relation in the community, requires much deeper and much more extensive study than it has received heretofore.

A CONCISE SYNOPTIC SURVEY.

As each main section possesses its own set of conclusions, it is unnecessary to do more than summarise the outstanding features in the four main fields discussed:

Succession. Succession is due to biotic reactions only, but we must admit the existence of succession-acceleration-retardation-deflection, interruption-postponement, and termination (Phillips, 1934, p. 568). Succession is progressive only, and the natural basis for classification is development.

Development. Development is due to biotic reactions only, and is progressive only; the process is best understood in terms of the complex organism concept of the biotic community.

The climax. The tendency of biotic communities to develop to a climax is emphatic; this climax is under the master regulation of climate, but as there is no other kind of climax it seems desirable to drop the adjective "climatic". The climax is in dynamic equilibrium not static adjustment with the habitat, and often consists of a mosaic of types. It is the fundamental unit of biotic communities or of vegetation, and hence is the natural basis, along with development, for classification of communities. Obviously the climax concept, based on the concepts of succession and development as above outlined, is innately associated with the concept of the complex organism.

The complex organism. The concepts of emergent evolution, holism and the complex organism are intimately related; the biotic community is a complex organism. The whole at different levels is an operative factor in the life of the biotic community. So far from the concept of the complex organism being either far-fetched or of theoretical value only, it is deemed to be of fundamental philosophical, scientific and practical value. In ultimate analysis it is the foundation for a natural classification of succession, development and the attaining of dynamic equilibrium in the climax.

I earnestly invite criticism, destructive and constructive, of the views expressed. I hope to present later a definitely *critical* treatment of the various concepts, theses, and general views mentioned in this series of papers.

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CONTROLLING FACTORS IN THE FORMATION OF FEN DEPOSITS, AS SHOWN BY PEAT INVESTIGA- TIONS AT WOOD FEN, NEAR ELY

BY H. AND M. E. GODWIN AND M. H. CLIFFORD.

(*Botany School, Cambridge.*)

(*With Plate XXXVIII and eight Figures in the Text.*)

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INTRODUCTION.

THE extent and position of the Fenland basin of East Anglia is shown by the map of Fig. 1. It is a shallow depression eroded over most of its area in the Jurassic or Cretaceous formations which in this area consist mainly of clay. On this floor there are local deposits of Glacial gravels and of boulder clay, but over the whole area there are extensive post-Glacial deposits consisting of alternating beds of estuarine silt or clay and of peat. The general features of the geology were admirably outlined by Skertchley in 1877 (1), but no more exact work had been pursued until the formation in 1932 of the Fenland Research Committee for the investigation of all aspects of the history of the Fenland basin. This paper is one of the firstfruits of the work of the Committee, and has inevitably rather the character of reporting progress than of stating final or fundamental features of fenland geology and history. The position could hardly be otherwise, because each site investigated geologically, archaeologically, historically, botanically or otherwise within the area must finally be made part of one general correlated schema, and this matter must occupy specialists for many years. At the same time no apology is needed for using Wood Fen as

an introduction to some of the problems of Fenland development. In the first place the attention paid to it by Skertchley has made it rather a classic site for the demonstration of the buried forests of Fenland, and in the second place it affords opportunity for correcting understandable but misleading errors in Skertchley's account and of establishing certain general principles which should prove of value in further stratigraphical investigations of the fens. Such principles could hardly receive proper emphasis in a long general paper correlating results from many Fenland sites.

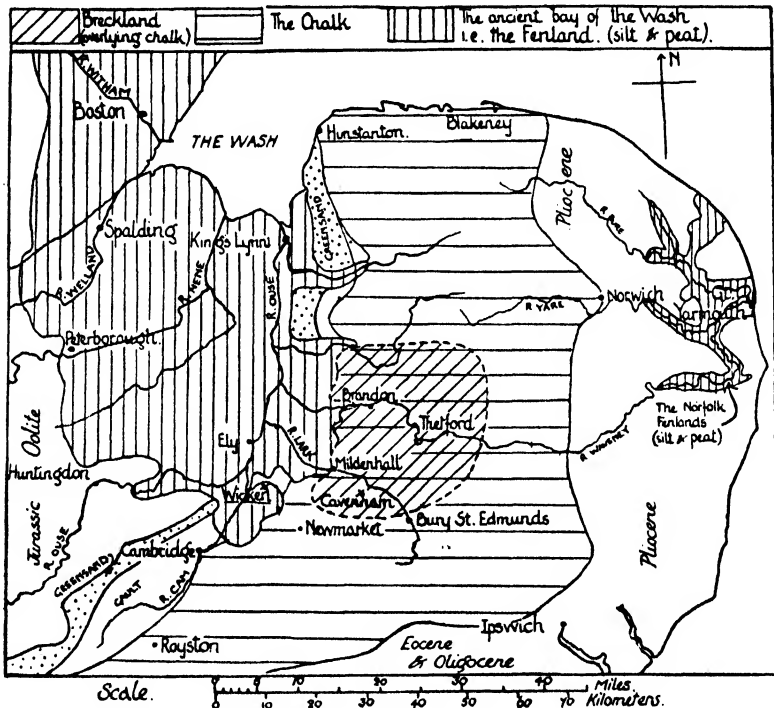


FIG. 1. Map of East Anglia showing the position and extent of the Fenland basin and its chief waterways. Wood Fen lies immediately north of Ely.

The present writers have had the advantage of employing in their peat investigations the recently developed technique of pollen analysis (2) which was not available to Skertchley.

POSITION, DRAINAGE AND SURFACE LEVEL.

Wood Fen lies 3 miles to the north of Ely (see Fig. 1), and occupies the triangular area between the clay hills carrying the villages of Littleport and Little Downham, and the smaller rise known as Brick Hill (see Fig. 2). Wood Fen is contiguous to the west with North Fen, and the two terms are sometimes employed for the same area: thus Skertchley in his "Geology of the Fenland"

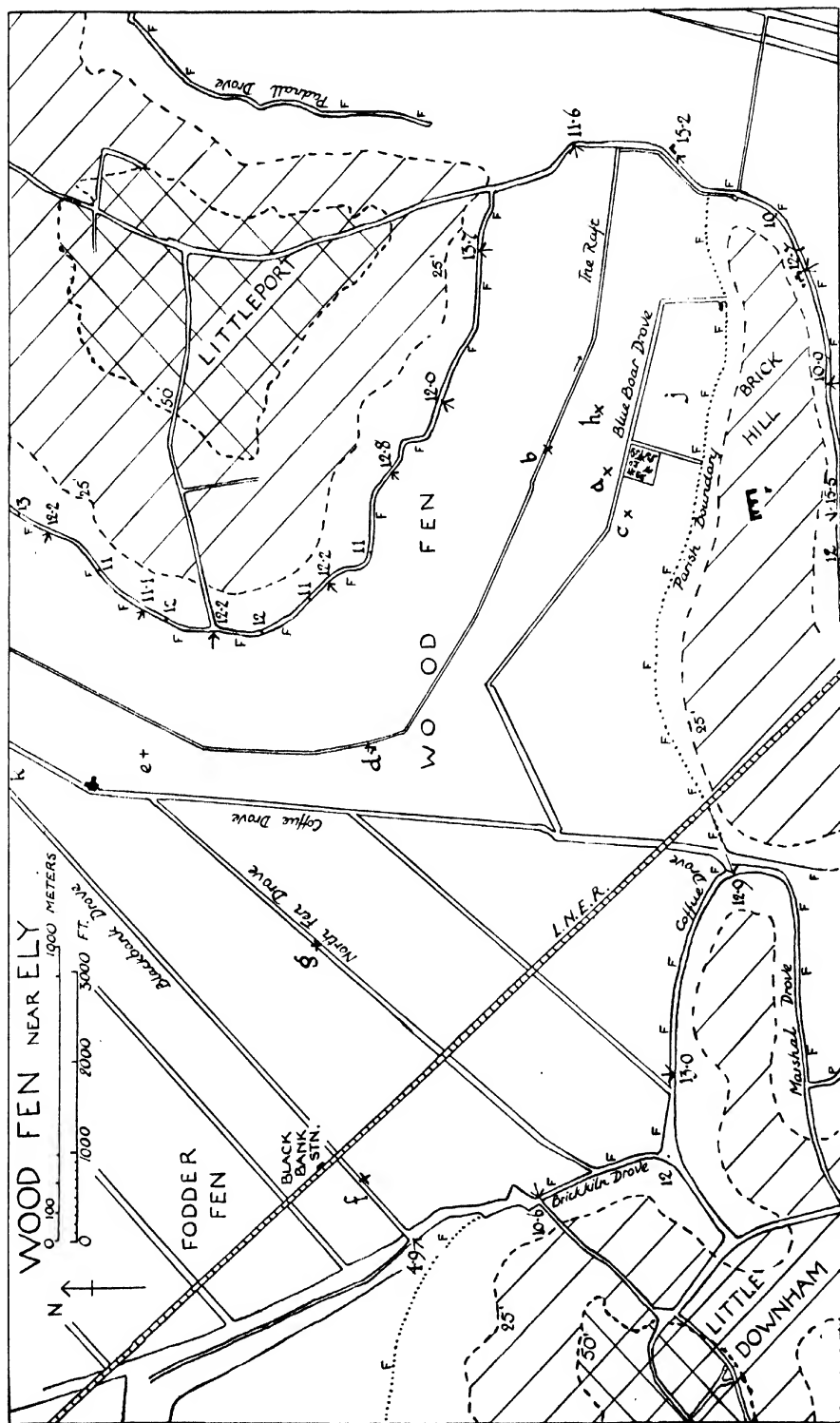


FIG. 2. Map of Wood Fen showing its position between the low clay hills of Littleport, Little Downham and Brick Hill. The sites alluded to in the text are shown by a letter and a cross. The line of the fen boundary is shown by a chain of the letter F. Where this line corresponds with a line of levelling by the Ordnance Survey the spot-levels and bench-mark levels are also given (in feet). The fen boundary follows the 10 ft. contour closely.

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(1) quotes a particular sequence in the buried forests of Wood Fen as given by Mr Marshall of Ely, whilst in *Fenland Past and Present* (3) he gives a figure of the same buried forests drawn by Marshall and labelled as representing North Fen.

The chief drain of this fen at the present day is the "Raft", which runs parallel with the contours of Littleport Hill. For the following account of the history of the drainage of Wood Fen I am indebted to Major Gordon Fowler, who is Vice-President of the Fenland Research Committee and who is actively engaged in working out the development of both the artificial and natural drainage systems of the fens.

Under the authority of "The Pretender Act" of 29th May 1649, Sir Cornelius Vermuyden, Director of the Company of Adventurers, carried out a general drainage scheme in the Fens. One of his minor works in 1651 was the cutting of a drain from Grunty Fen northwards round the west side of Ely and Littleport highlands to the main river near the latter village. This drain passed along the west side of Wood Fen and must have drained it to some small extent till about 50 years later the ensuing wastage of the peat over the whole district made the drain, which relied upon gravity for its discharge, ineffective and wintertime marshy conditions returned. One can presume that it remained in such a condition till shortly after the passing of the Littleport and Little Downham District Internal Drainage Act of 1755—amended in 1799, 1809 and 1878. Wood Fen then became part of one of the 26 old subdivisions of that district and like most of the others probably had a little windmill to scoop the water out of its own drain into the main drain of the district, which went westward to the bank of the 100 Foot or New Bedford canal where a larger mill lifted the water into the tide-way. Ever since then the drainage of this Fen has been westward to the 100 Foot canal. The drains running round the highlands on the north and south sides of the Fen are catchwaters, the latter of which was not made till 1842, and discharge eastward into the main river.

The general history of this and similar local Fens indicates that the windmills were effective only as long as means could be taken to increase their lift in proportion to the wastage of the peat that followed drainage and subsequent lowering of the water level in the necessarily deepened drains. Being at the mercy of the winds, at no time could the mills have been reliable.

The last main drain windmill of the district, on the 100 Foot Canal Bank, was replaced in 1818 by a 30 H.P. steam engine driving a scoop water wheel. A second steam engine was placed there in 1830. The diameter of its wheel was 41 feet, but owing to the above-named causes it had to be replaced in 1882 by a 50 foot wheel driven by an 80 H.P. engine.

A responsible living witness testifies that at about this time Wood Fen was often waterlogged in the winter and that his father, who lived to a great age, told him it was due to the fact that in his early days it was considerably lowered by turf cutting.

A more powerful steam engine driving a centrifugal pump was installed on the 100 Foot Bank in 1914 and appears to have provided the district with its first really efficient drainage. Since then the wastage of the peat has gone on apace and the cultivators of Wood Fen have had to work hard to keep it clear of the old subterranean forest trees as the land wasted down on to one after another of their horizons.

In 1927 a powerful semi-diesel engine was placed alongside of the 1914 steam engine and now helps to keep the water of the district at a very low level.

G. F.

It has been very clearly shown by Fowler (4) that since the initiation of artificial drainage in the fens the surface of the peat land has become progres-

sively and rapidly lower. This has been measured by a whole series of indices, of which the best are probably the records of deepening of the outfalls of drains, and the exposure of the iron column sunk at Holme Fen in 1851 when Whittlesea Mere was drained. A lowering of about 1 in. per annum seems to be a very general figure for the recent period of intensive drainage. This rapid change in surface level is strikingly shown in the map of Fig. 2, in the position and level of the old fen-margin roads. These in all cases skirt the uplands closely parallel with the 25 ft. contour, and spot-levels on the roads themselves and benchmarks on buildings beside them lie, as can be seen in the figure, very closely about +10 ft. o.d. (Newlyn). Such roads partly encircle the Littleport upland (and are continued by Padnall Drove), run along the south side of Brick Hill, though replaced on the north side by the deep fen-margin ditch which is the parish boundary, and finally they circle the Little Downham upland as Marshall Drove, Coffue Drove and Brickfield Drove. The 6 in. maps show that the system of fen drains always extends to the line of these fen-margin roads, and this indeed could have been inferred from the term "drove", which is used for a fen road. It would thus seem extremely probable that the fen here formerly reached a general level of about +10 ft. o.d. This is not seriously out of agreement with the present surface level of Wicken Fen (+7.0 ft. o.d.)¹, which, though undrained, has nevertheless a controlled upper level above which the peat cannot grow, and where peat-cutting has certainly taken place in the past (5). A levelled traverse has been made from south to north across part of Wood Fen from the parish boundary, through sites *a* and *b* to the Raft, and the result shown in Fig. 3 gives a very clear idea of the present level of the fen surface. The centre of Wood Fen now has a surface level of -2 ft. o.d. at sites *a* and *b*, whilst other levelled sites, *d*, *e* and *f*, also have surface heights between 0 and -3 ft. o.d. At the same time, near the boundary ditch on the south side of the fen, the peat surface level rises gradually to +7.0 ft. o.d. (see Fig. 3). Extensive levelling in Wicken Fen and observations in the peat areas of the Norfolk Broads do not suggest that such a curvature could have been present during growth of the peat, which certainly depended on a maintained high water-table; and this over distances of the order here involved must itself have been quite flat. It seems extremely probable then that 200 years of drainage have lowered the peat surface by something of the order of 10 ft. This is quite in agreement with the findings quoted by Fowler and generally recognised for the Fenland.

Since we have to consider in this paper the stratigraphy of the peat now remaining in Wood Fen, it is necessary for us to consider whether the phenomenon is one of shrinkage and compression (in which case the whole of the original peat sequence will be preserved though in much reduced thickness), or alternatively of surface wastage (in which case the more recent surface layers

¹ Wicken Fen lies 9 miles due south of Wood Fen and peat fen stretches continuously between the two areas.

of peat will have been progressively removed, leaving the older layers only). The necessity for such a distinction has not up to the present been adequately stressed. The former of the two alternatives was formerly adopted, but it appears much more probable that the second of these hypotheses is correct. As the high water-level by preventing decay led in the first place to peat accumulation, so the lowered water-table, by allowing access of air to the peat, initiated the aerobic processes of direct and bacterial and fungal oxidation and breakdown which finally must cause conversion into little more than carbon dioxide. A small amount of shrinkage is no doubt often present also, but this will vary much and will not generally be the major component.¹ If this view is correct "wastage" is the better term to apply to the process resulting in

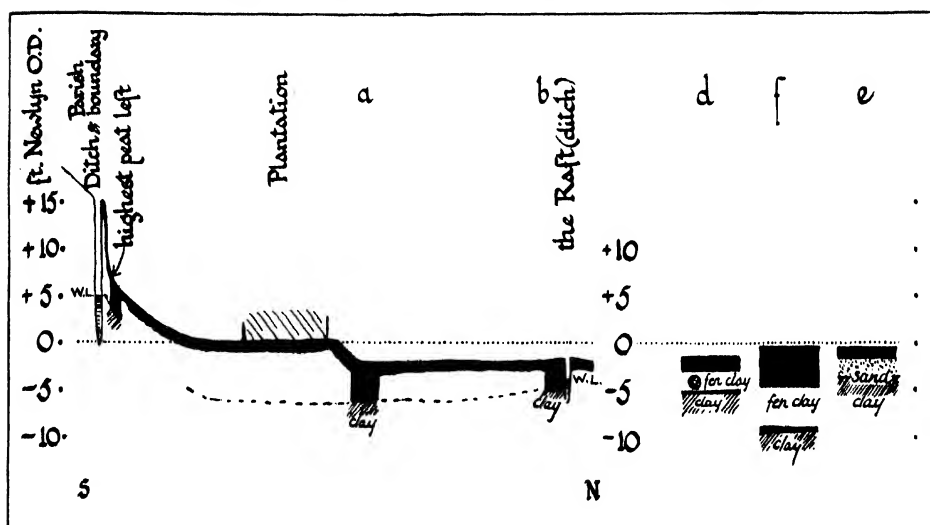


FIG. 3. Diagram of a levelled transect from south to north from the fen margin of Wood Fen to the centre, passing through sites *a* and *b*. For comparison the sites *d*, *e* and *f* are shown also at their ascertained levels. The peat surface of the centre of the fen is below mean sea-level but curves upwards above it at the margin.

lowering of the peat level. We must expect to find recent peat profiles only in those parts of the Fenland which have been preserved from the intensive draining either by human control or, in the seaward lying areas, by the protection due to overlying beds of fen silts and clays.

THE BURIED FORESTS.

Though familiar in the marginal peats of the whole Fenland basin, buried forests are nowhere better shown than in Wood Fen, where they were very thoroughly investigated by Skertchley and Marshall. These authors satisfied

¹ It is not intended to suggest that during the formation of peat there is not very substantial compression such as that involved by squeezing out of water, but to emphasise that this factor is of minor importance when the already consolidated material of mature bogs is exposed to surface drainage.

themselves of the presence of no fewer than five distinct forest horizons in the arrangement given below.

- (v) Alder-willow-sallow.
- (iv) Pine.
- (iii) Pine.
- (ii) Oak-yew.
- (i) Oak.

Of these only the lowest forest was rooted in the basal clay; the trees of the other horizons were rooted in the peat and showed strikingly horizontal root systems, a feature no doubt due to growth in a shallow peat layer immediately over the water-table. Exactly similar root systems can be seen at the present

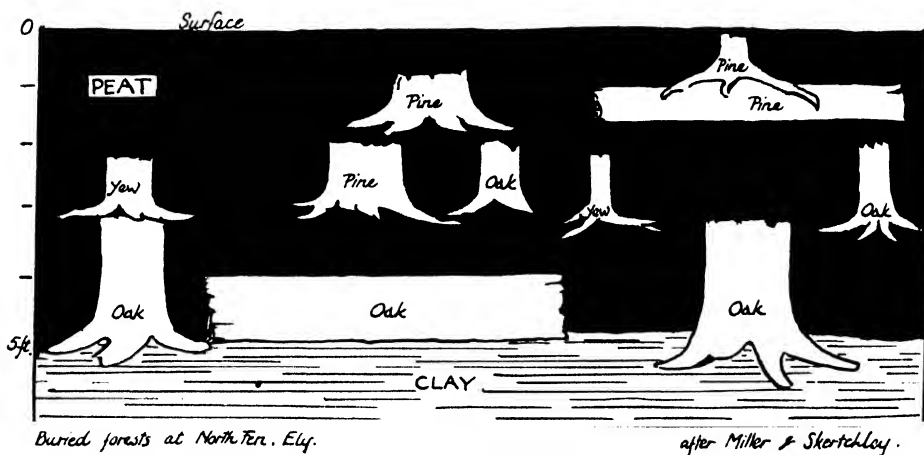


FIG. 4. Diagram after Miller and Skertchley showing the succession of buried forests at North Fen (continuous with Wood Fen or in part synonymous). The four lower horizons only are shown, viz. (1) Oak, (2) Oak-Yew, (3) Pine, (4) Pine. The fifth and uppermost is omitted.

day in wind-thrown oak trees which grew in deep peat on the Norfolk Broads (see Pl. XXXVIII).

The forest sequence is clearly illustrated by the diagrammatic section drawn by Marshall and reproduced in Fig. 4. Two features are particularly striking; firstly the actual occurrence of both pine and yew growing in Fenland peat, and secondly the manner in which the trees of one horizon may be found with their roots astride and even clasping the fallen or upright trunks of trees in the horizon below. Both these facts, as also the general sequence of buried trees, are easily confirmable at the present day by a winter visit to Wood Fen, where the farmer is constantly excavating the stumps of the buried trees which snag the plough. Now, however, the upper horizon of alder, willow, sawallow is no longer easily recognisable, a result, no doubt, of surface peat wastage, and the excavated trees are almost entirely pines. As Marshall and Skertchley say, the fallen trunks mostly lie in a south-west-north-east direction, and this they

attribute, probably correctly, to the prevalent tree shape developed by winds blowing in the same direction as now. The pines are well preserved, and long and

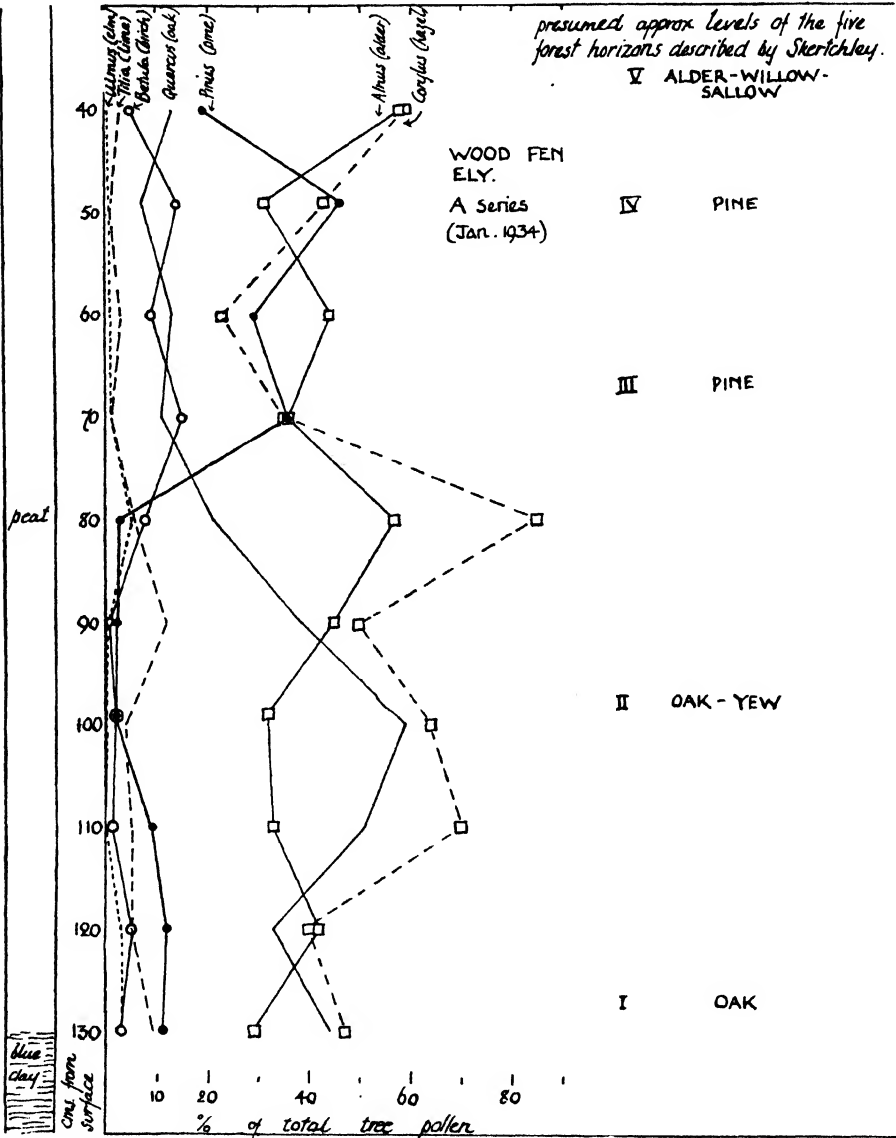


FIG. 5. Diagram showing the results of analysis of tree pollen in a vertical series of samples from site a. On the right are inserted the presumed levels of the five forest horizons described by Marshall and Skerchley. They all appear to be clearly indicated by the tree pollen spectra.

straight, showing former forest growth, and the yews, here growing on peat, are smaller, though much larger yews are found below peat growing upon sand or weathered Jurassic clays, as on the margin of Wood Fen itself at the north end

of Blackbank Drove. The presence of both pine and yew is of particular ecological interest, since neither is commonly regarded as capable of constituting woodland on deep topogenous peat.¹ *Pinus sylvestris* is regarded as limited to dry and poor soils, and shallow acid hill peats... this fossil occurrence accords more with the free growth of this tree in plantations on the topogenous peat both of Fenland and of the Norfolk Broads (1). It agrees closely with the occurrence of the pine as a regular component of "Zwischenmoor" and the later stages of formation of "Hochmoor" from the lacustrine peats of the shallow lagoons of the north-west German coast (see Steffen (7)). It seems probable that *P. sylvestris* has been in the past, and possibly is now, a normal constituent of the woodland developing on topogenous peats, though, as will be shown later, not necessarily whilst it still remains alkaline in reaction. There is unfortunately inadequate fossil material for the determination of the exact systematic position of the pines. A few cones have been found and are illustrated in Fig. 6. Beyond this there is the thick bark and the straight form of the trees, but these characters are together inadequate for answering the very interesting question of whether the fossil pines are related to the native Scots pine (*P. sylvestris* var. *Scotica*), to the continental race of pine now spontaneous in East Anglia, or to some other group. *Taxus baccata* is regarded, even less than *Pinus sylvestris*, as a tree of peat soils, since it is now naturally abundant in this country only on dry calcareous soils. However, its presence in Wood Fen, rooted in peat, is indubitable, all the wood is clearly recognisable and male sporophylls (Fig. 6a) have been found at sites *a*, *c* and *d*. Other small rooted yews have been found in Methwold Fen growing over several feet of topogenous peat. This evidence would seem to establish beyond doubt the status of the yew as a former natural constituent of the native fen woods.

In discussing the lowest tree horizon Skertchley comments on the manner in which the roots of the oak trees seem always to be situated on a mound in the stiff clay. This the present writers would suggest is due to nothing more than the normal raising of soil level round the foot of any large tree. It is due to the upwards displacement of the surface soil by the penetration and growth of a very large bulk of thick tree roots, and may be seen in any parkland when the turf is short enough for the soil contour to be recognisable.

SITE A.

(1) *Tree pollen.*

Samples for analysis were secured by a Swedish peat sampler at 10 cm. intervals from a depth of 40 to 130 cm. After alkaline maceration the larger fragments, mostly identifiable only underneath a microscope, were strained off, and the residue was mounted for pollen analysis. The analyses for tree pollen and hazel are given in Fig. 5 and it will be seen at once that it reflects

¹ Topogenous peat is that formed through the accumulation of drainage water in a basin-shaped area.

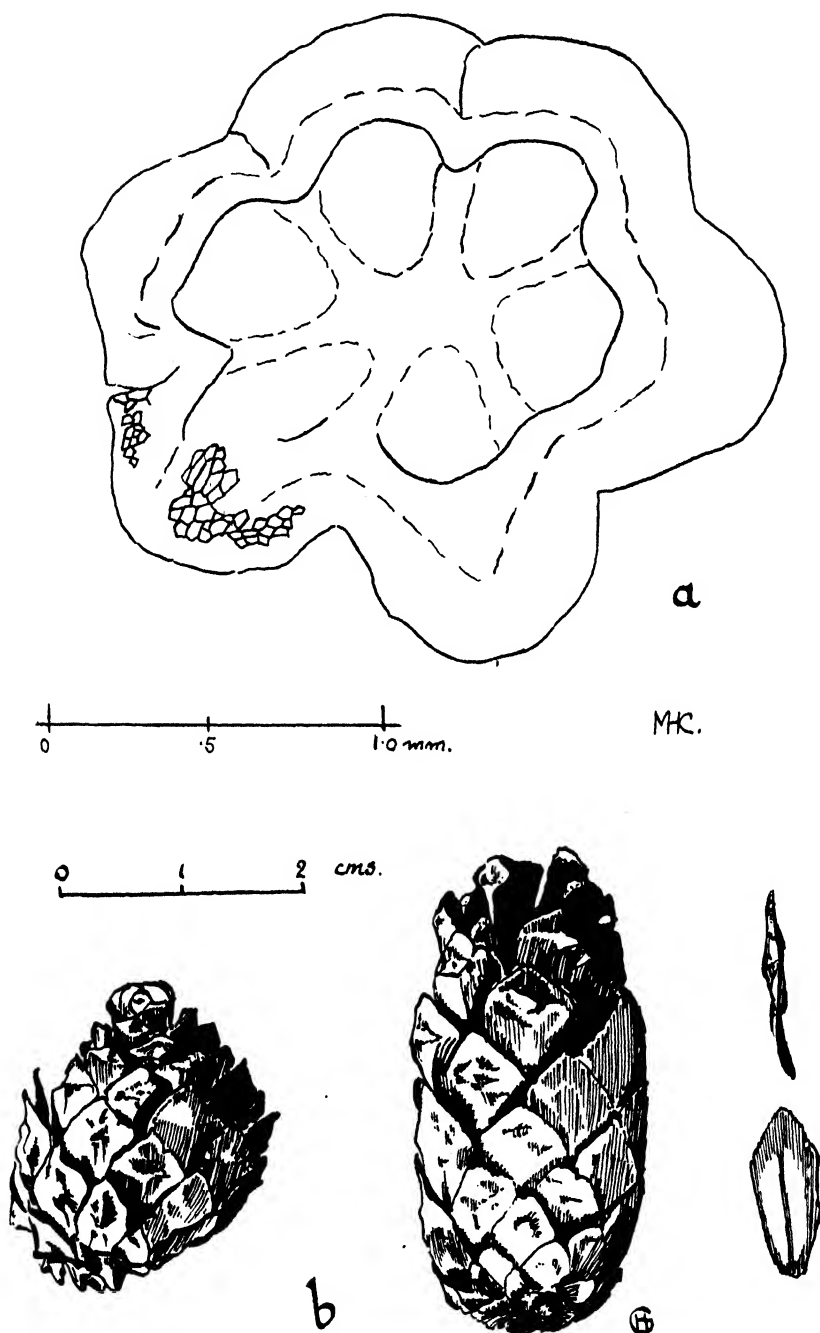


FIG. 6. *a* shows the male sporophylls of *Taxus* recovered from samples at 45 cm. from the surface at site *d*. *b* shows sub-fossil pine cones from Wood Fen. It will be seen that the apophysis is thin and belongs to the "*plana*" type.

important changes in tree composition throughout the peat bed. In the lower half oak and alder pollen are co-dominant, in the upper half pine and alder, with the tendency expressed in the uppermost sample for alder alone to dominate all the other tree pollen. With the rise in pine pollen, birch pollen shows a corresponding but smaller increase. This sequence reflects very faithfully the forest sequence worked out by Skertchley and Marshall, and the presumed levels of the five forest horizons have been included in the diagram at appropriate heights. It is to be noted that no trace of the pollen of *Taxus*

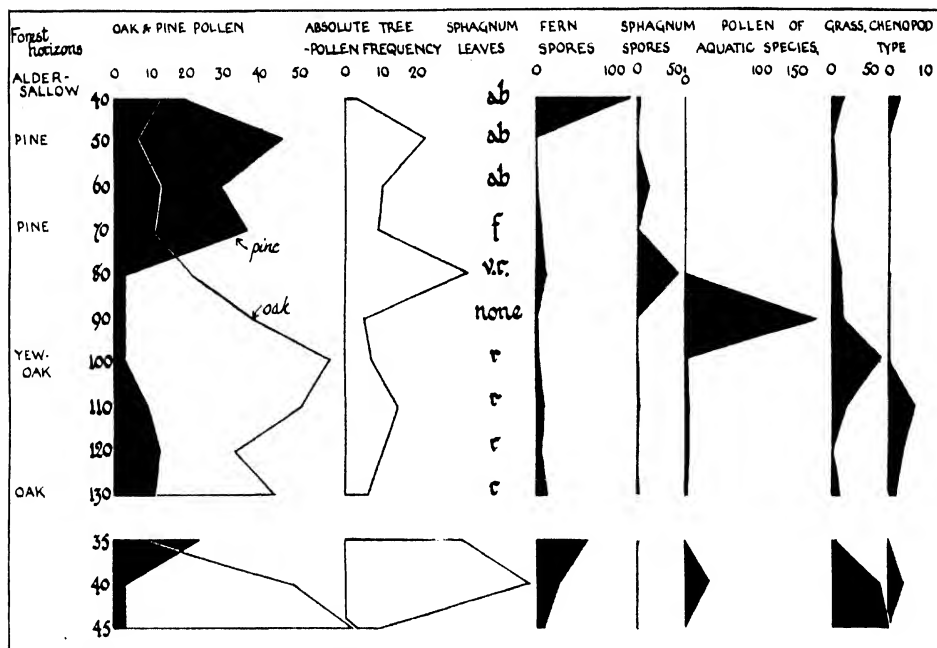


FIG. 7. Pollen analyses and results of examination of other micro-fossils from site *a* (above) and site *d* (below). On the left for comparison are given the pine and oak pollen values throughout the whole vertical series. In the series from *a*, note the sequence of maxima in the non-tree pollen and the correspondence of the disappearance of *Sphagnum* leaves at 90 cm. with the maximum of aquatic pollens and the period of transition from oak forests to pine.

was observed: this agrees with the general view that yew pollen is extremely subject to decay. The tree pollen assemblage includes, besides the genera mentioned, also *Ulmus* and *Tilia*, though the fluctuations in their frequency and in that of the *Corylus* pollen do not call for comment at this stage.

(2) Pollen other than tree pollen and other spores.

The non-tree pollen and spores which were counted at the same time as the tree pollen, yielded the interesting results set out in Fig. 7. In each case the amount of non-tree pollen is expressed as a percentage of the total tree pollen, and it will be seen that the curve for each type has a well-expressed maximum.

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These maxima are, in order: at 110 cm., *Chenopodiaceae-Alsineae* type pollen; at 100 cm., gramineous pollen; at 90 cm., a very pronounced maximum in the pollen of aquatic genera such as *Typha*, *Sparganium* and *Potamogeton*; at 80 cm., *Sphagnum* spores; and at 40 cm., fern spores.

(3) *Other micro-fossils.*¹

The remaining micro-fossils are set out in the subjoined table.

Cm. below surface	<i>Alnus</i>	<i>Quercus</i>	<i>Taxus</i>	<i>Other wood</i>	<i>Phragmites</i>	<i>Cladium</i>	<i>Carex</i> roots	<i>Scirpus</i>	<i>Batrachian</i> seed	<i>Charales</i>	<i>Fern</i> sporangia	<i>Mosses</i>	<i>Sphagna</i>
40	+	.	<i>S. cymbifolium</i> + a narrow celled species, abundant
50	+	<i>S. cymbifolium</i> , abundant
60	+	<i>S. cymbifolium</i> , abundant
70	<i>S. cymbifolium</i> , frequent
80	+	.	+	<i>S. cymbifolium</i> , very rare
90	+	.	+	+	Absent
100	+	.	.	<i>S. cymbifolium</i> , rare
110	.	.	+	+	<i>S. cymbifolium</i> , rare
120	.	.	.	+	+	.	.	.	<i>S. cymbifolium</i> , rare
130	+	<i>S. cymbifolium</i> and a narrow celled species, rare

These results are of particular interest because of the presence of *Sphagnum* leaves, especially in the upper half of the section. *Sphagnum* was absent only from the sample at 90 cm., the maximum of the aquatic pollen. This level also shows remains of *Phragmites* and roots of *Carices*, and the sample next below shows a *Chara* fruit.

DISCUSSION.

It has recently been emphasised by Overbeck (8) that in contrast to the tree pollen which is widely wind-blown, the non-tree pollen yields a very local picture indicative of conditions in the peat-forming bog itself. This is, of course, even more closely true for the leaf, stem, and root remains found *in situ*. And since we have shown the tree pollen to follow, as we should expect, the sequence of the forests buried in the peat bog, we may agree that all these fossils combine to give the best possible record of conditions of *the development of the fen itself*. It ought perhaps to be said at this stage that the buried forest horizons were readily verified in the neighbourhood of site *a*, as well as at site *a* itself, for the fossil trees outcropped in all the field ditches thereabouts.

The most striking feature of the fossil record is the abundance of *Sphagnum* which has not, so far as the authors are aware, been recorded hitherto from Fenland peats. The fen peats owe their origin to the topographical conditions,

¹ The term "micro-fossils" is here employed to mean the whole fossil content for the identification of which microscopic analysis is necessary. It includes fragments of wood, of leaf and root cuticles, seeds, sporangia and such like material, usually in pieces less than 1 cm. in length, since the peat samples are small and decay has been pronounced.



Phot. 1. Fen Oakwood growing on deep topogenous peat at Calthorpe Broad, Norfolk. Showing oaks 45 to 50 feet high, some of pioneer and some of semi pioneer form. Undergrowth of *Phragmites communis* (right) and *Osmunda regalis* (left foreground). In the background are bushes of the fen carr.



Phot. 2. An overturned oak in the fen Oakwood at Calthorpe Broad, showing the very shallow horizontal plate of roots. The fallen moss-covered fringe of outer roots is shown propped open by a spade. The tree is still living and new shoots are growing from the trunk. *Phragmites* is seen on the right. Mature trees of the fen wood and bush carr of alder, birch and willow are in the background.

which resemble those of a large delta into which the waters of large fenland rivers, the Witham, Welland, Nene and Ouse and their many tributaries are discharged. These streams drain areas of Jurassic clays often covered with boulder clay, and their waters are rich in bases, and must equally in the past as now have kept alkaline the vast amounts of topogenous peat they caused to develop in the fen basin. One of the present authors has already sought to show that in the similar topogenous peat area of the Norfolk Broads there is, even under those conditions of peat formation, a natural tendency for the peat to grow above water-level, where, being out of contact with alkaline water, it becomes increasingly acid, and bears characteristic acidiphilous species. Thus on deep topogenous peat at Calthorpe Broad, Norfolk, the surface peat away from the broad bears *Eriophorum angustifolium*, *Polytrichum commune*, *Mnium hornum*, and various species of lowland *Sphagna* (6). In other localities it is known that the peat becomes sufficiently acid to carry also *Calluna* (9).

This process of acidification is part of the bog-development series completely shown in many western continental countries, namely the transition from alkaline topogenous bog to neutral and slightly acid "Zwischenmoor", and finally to convex, *Sphagnum*-dominated, highly acid "Hochmoor". It seems probable that in the relatively continental climate of East Anglia the *Sphagna* cannot develop sufficiently freely to convert the "Zwischenmoor" into "Hochmoor", and the climax vegetation therefore remains a fen wood dominated by a mixed population of oak, alder, ash and other trees, such as are described on the continent as "Zwischenmoor-Mischwald". Semi-natural fen woodland approaching this character has been described for Calthorpe Broad and the photograph in Pl. XXXVIII gives some idea of the nature of this type of vegetation. Two or three generations of oaks are visible in the picture, so that the community is evidently of some permanence. The surface soil is acid and bears scattered tussocks of the less acidiphilous *Sphagna*, but there is also abundant growth of *Phragmites*, Carices and other species of "Flachmoor" type. We suggest that it is under conditions of this kind that most of the peat of Wood Fen (a) was formed, and it may be noted that *Pinus sylvestris* had been very successfully planted with the oaks in the fen woodland at Calthorpe, and there is some evidence that it may regenerate naturally there. It will also be recalled that the abundant species of *Sphagnum* (*S. cymbifolium*) in Wood Fen is one common in the German "Zwischenmoorwälder", and that we have already drawn attention to the horizontal root systems of the buried trees, suggesting that they are a response to a permanent high water-table.

We have so far drawn our evidence for the natural development of topogenous peats from the Norfolk Broads, but there is some evidence that Fenland peats also reached a condition of surface acidity and supported natural vegetation of an acidiphilous character. There is a particularly interesting

paragraph which bears on this in Miller and Skertchley: "Wells, in his *History of the Bedford Level* (1830), in his chapter on the 'Phenomena of the Fens, its Plants and Natural Productions', touches in the slightest manner, the Botany of the Fens; all he tells us is that 'the turf moors are covered with such plants as the Heath, Ling, and Fern. The *Myrica Gale*, plants and natural productions, and a grass with a beautiful white tuft called the Cotton grass, are found in abundance.' The Cotton Grass (*Eriophorum angustifolium*) was, forty years ago, a conspicuous feature of the Fens, but it lingers now only in a few places. The rest of the statement is incorrect. The old surface of the Fens was nowhere in Mr Wells' time, or probably at any time covered with Heath, Ling and Fern, and those who knew Mr Wells as intimately as the present writer, will think it no detriment to his acknowledged ability in all matters relating to the History of Fen Drainage, that he should not have regarded the Fens with the eye of a botanist." Here is clear enough evidence of the former widespread occurrence of cotton grass, which, if not *highly* acidiphilous, nevertheless indicates conditions near neutrality or on the acid side of it. And if so much be granted, may Mr Wells not have been nearer the truth in his statements than Marshall (above) supposed? That *Eriophorum* has now disappeared from almost all the fens is evidently due to the drainage and the peat wastage, which, as we have said, has removed as much as 10 ft. from the peat surface. First of all to go would be the latest most acid peat, and with it the acidiphilous species, now brought by lowered soil-level within reach of floods of alkaline fen water which would be inimical to such species. Certain marginal tracts of fen, little subject to drainage or turf-cutting, have indeed retained traces of an acidiphilous vegetation even to the present day, and in the neighbourhood of Holme and Denton Fens, *Calluna*, *Erica* and *Eriophorum* still grow on the old fen surface. The insect records point equally distinctly in the same direction. "Few records exist of heath or moor insects, but even were there no other evidence, they are sufficient to prove the former existence of a heather-studded moorland in the Fens" (3). *Celoena Haworthii* (Haworth's minor), which feeds on cotton grass, was once abundant and has now disappeared; *Anasta myrtilli* (the Yellow Underwing), which feeds on ling, could still be taken in Holme Fen in 1878. Even Wicken Fen, which now yields no ground at all acid, was the site for which was first recorded in England *Trichoptilus paludum*, an extremely specialised insect feeding on the tentacles of *Drosera*. There seems no botanical record of the presence of sundew in Wicken, but it is practically certain that it must have existed there and that therefore acidic soil conditions were also present. It seems likely that such neutral and acid peat had in fact formed widely over Fenland, especially marginally, at the time of the commencement of artificial drainage, and it is quite probable that at first drainage would have even emphasised this tendency of soil development. Nevertheless it has in the end certainly destroyed almost all the evidence that such types of peat ever existed in the fens.

The woodland conditions we have described for our fen "Zwischenmoorwälder" are by no means dry and need not in our opinion indicate a period of increased dryness of climate. They are merely the sequel to the natural processes of vegetational succession of which they mark the natural climax under present-day climatic conditions. The rate at which such a woodland stage will be reached in fen areas will naturally depend upon the depth of water in which peat formation begins and the areas which will soonest reach the climax woodland stage will be those marginal areas where only a few feet of peat growth is needed to bring the ground surface above the general water-level. In some cases it may be that peat did not form in any depth of water, but that peat-growth and water-logging accompanied one another and progressed together. Even so, topographical differences would affect the ease of water-logging and some sites would reach a woodland phase far more rapidly than others. These facts are doubtless the explanation of the distribution of buried forests shown by Skertchley in his maps of Fenland; he remarks that everywhere they are to be found on the margins of the uplands. The reason for the rich development of these forests in Wood Fen lay doubtless in its position on a saddle between low hills and rather removed from the influence of the main drainage channels of the deeper fens around. We should expect on our hypothesis that marginal woodland would develop freely at a time when, in the central Fenland, vegetational succession was still in its early stages and only alkaline swamp peat was being laid down. In the course of time the trees of the fen-woodland would die and fall, becoming incorporated in the slowly growing peat. The continued growth of the peat necessary to bury the trees would follow in part from the gradual compression of the soft swamp peat below the forest, which, in its early stages at least, might be actually floating on semi-liquid peat. In part, continued peat growth might be due to a general rise of water-level in the area, following either impeded drainage or some externally operating factor such as coastal movement or increasing rainfall. In the process of burying by the growing peat prostrate trunks would be exposed long enough for the bark on the upper side to decay away, whilst that on the lower would be preserved. This is the condition of the Wood Fen trees. According to this view of the origin of buried forests the superposition of one layer of trees growing *in situ* above another, as at Wood Fen, need indicate no climatic or edaphic change. A similar view has been extremely well expressed by Penhallow in his investigations on the buried forests in the peats of the Atlantic coast of Canada (10). There are two forest horizons, and of their origin he writes as follows. "It would seem that the young forest of white pine . . . grew upon the somewhat unstable base afforded by the 'quaking-bog' shortly after emergence from the Cassandra stage. This condition is exactly duplicated today by neighbouring bogs, where white pine trees of about the same size may be seen in direct succession to the Cassandra. With an increasing weight of the surface mass, this latter was carried down to a lower

level by its own weight, and to such a position as once more to re-establish aquatic conditions. It thus became necessary for the bog once more, but for a brief period only, to pass through those phases of development previously completed. Without the repetition of such a catastrophe, the bog continued a normal development until a second forest of white pine had attained to an age of one hundred years or more." We should differ from Penhallow in suggesting that under some conditions there need be nothing catastrophic in the submergence of the forest horizons by the growing peat. Several layers of trees may thus accumulate above one another under constant external conditions, provided that these are favourable for continued peat formation. This at once raises the issue of the exact significance of the five forest horizons distinguished by Marshall and Skertchley: there is no doubt that it must have been a matter of great difficulty to decide on the exact number, since many of the trees are 1 ft. or more in diameter, and the thickness of the peat bed is only 5 ft. in all. It will be most profitable at this point to re-examine the micro-fossil data for exact evidence of the progress of fen development, so as to formulate a coherent picture correlating both fen and forest growth. Skertchley supposed the successive forests to be due to land movements of elevation and depression relative to sea-level, trees growing in the former periods and being killed out by renewed peat growth in the latter. The non-tree pollen and other micro-fossil content, however, gives no evidence of such a fivefold repetition of phases. There is, on the contrary, in the non-tree fossils evidence for *one* change of particular importance in the centre of the bed. This is the sequence of maxima in Chenopodiaceae-Alsineae, in Gramineae, in pollen of aquatic species and in *Sphagnum* spores. Though the evidence is yet incomplete it seems likely that the Chenopod-type pollen is indicative of the deposition close to the Fen of the semi-marine fen clay. A similar maximum of Chenopod-type pollen was found at the base of peats just overlying semi-marine clay at St German's, near King's Lynn, and was there explained as due to salt-marsh plants (11).

The gramineous pollen probably represents, like the similar maximum at St German's (where there is direct evidence for the change), part of the transition to fresh water, though whether attributable to grasses of brackish water reed-swamp, such as *Phragmites communis*, it is not possible to say, since the different grass genera and species are not identifiable from their sub-fossil pollen. These open fresh-water conditions must have reached very close to site *a* in Wood Fen, for cessation of *Sphagnum* peat formation coincides with the maximum of aquatic pollens. This phase is followed by renewed growth of *Sphagnum* peat as indicated by the maximum of *Sphagnum* spores and later by the abundant *Sphagnum* leaves. The lowest forest layer rooted in clay has claim to be separated from the peat forests, and the upper alder-sallow-willow phase seems indicative of a return of rapid peat growth and retrogression from forest to an earlier seral stage of fen vegetation. With these facts in mind the sequence of fen development may be analysed as follows:

Forest horizons	Conditions at site <i>a</i>	Conditions in deeper parts of Wood Fen near site <i>a</i>	Relative movement of land and sea
v Alder-sallow-willow	Reversion towards aquatic conditions	Alkaline peat possibly without trees	Submergence (or increased rainfall)
iv Pine stumps	Acid Zwischenmoor peat	Alkaline peat	Stability or elevation*
iii Pine stumps	Acid Zwischenmoor peat	Alkaline peat	
	Aquatic phase and alkaline peat	Open-water and aquatic plants Brackish water Semi-marine fen clay	Submergence
ii Oak and yew stumps	Slightly acid Zwischenmoor peat	Alkaline peat	
	Peat growth begins in the oak woods		Submergence (or increased rainfall)
i Oaks rooted in clay			Stability or elevation*

* Under the term "stability" may be included such slackening of the submergence rate as would allow the constructive vegetational processes to gain the upper hand: it is possible, on this evidence, that the whole sequence is explicable as a process of depression continuous but varying in rate. On the other hand, further geological evidence in the fens appears to indicate elevation at certain times.

There would seem no mechanism for explaining the incursion of semi-marine clay save marine invasion and if we postulate a similar cause for the final return of aquatic conditions, the fen development would appear to indicate a first period of stability or elevation, a first period of submergence, a second period of stability or elevation and finally a second period of submergence. There seems little doubt that even if Skertchley was hardly correct in attributing the death of the trees to peat growth (which more strictly in our view merely covers trees which have died naturally), he was right in ruling out wholesale felling by human beings, and destruction by fire as primary agents responsible for the death of the trees. Though burned pine stumps are recovered from apparently undisturbed peat, it is rather the exception than the rule and may still possibly, as Skertchley suggests, have to do with quite recent peat burning. The view that no catastrophic agency need be invoked to explain the origin of a buried forest receives support from the results of pollen analysis through a forest containing peat at St German's. Pollen samples below and above the fallen oak trunks showed no sudden break in peat-forming conditions but fell naturally into place in a vegetational sequence readily interpretable as succession from alder-carr to oak fen-wood.

The view here taken is then that the Wood Fen profile *a* covers two periods of elevation or stability and two of submergence in contrast to the five periods of each suggested by Skertchley. The forest horizons recognised by Marshall and Skertchley are confirmed, but probably should be reduced from five to four in number by treating the Pine forests as one rather than two horizons. It should be noted that at the period of development of *Sphagnum* peat the fen surface must have been high enough to be out of reach not only of sea water

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but also of the alkaline fresh water held up by the tide. The pine forest layer is now about -3 to -5 ft. O.D. (Newlyn), and if we assume a tidal range of 20 ft. in the Wash, then Wood Fen must have been, when this layer was forming, at least 15 ft. (more probably 20 ft.) higher above sea-level than now. This calculation neglects the factor of peat-compression below the pine horizon, but compression to 50 per cent. of the original thickness would diminish these figures by less than 2 ft.

OTHER SITES.

(1) *The centre of Wood Fen.*

We have so far examined only the stratigraphy of what may be called the type site *a*, at centre of Wood Fen, where peat rests directly upon a much older pre-Quaternary surface or on boulder-clay. This site together with sites *b*, *c*, *h* and *j* may be considered as typical sites for Wood Fen (itself however a marginal fen), the remainder, *d*, *e*, *f*, *g* and *k* are referred to as outlying sites. The excavation of site *c*, without pollen analysis, showed a comparable profile, as the section on p. 527 indicates.

These results appear to indicate clearly the following stages of local bog development (in order of time):

(i) accumulation of alkaline fen peat of reed swamp type, 165-105 cms. (absence of *Sphagnum*, abundant *Phragmites*, *Carices* and *Characeae*) with encroachment over marginal alder, or local alder carr.

(ii) Transition to acid "Zwischenmoorwald", 105-80 cm. (abundant *Sphagnum* in pockets, sparser *Phragmites*, abundant remains of alder, birch, willow (?))

(iii) Phase of halt in the acidification, 80-65 cm. (absence of *Sphagnum*).

(iv) Progression to acid "Zwischenmoorwald" again, 65-45 cm. (presence of alder and birch remains and increased amounts of *Sphagnum*).

This accords remarkably well with the general scheme of development we have postulated for site *a*, though in site *c* the period of formation of the fen clay seems to have caused but a minor break in the bog development. Of the two pine stumps exposed in the section the upper clearly belonged to the later "Zwischenmoor" phase; the lower one may also have belonged to this phase, or possibly to the preceding phase of more alkaline peat.

At site *b* again 3½ ft. of peat rested directly upon the basal clays of the fen basin, and at site *h*, where a large pine was exposed in a field drain, a peat sample from immediately below the standing stump gave the following results of pollen analysis:

Pinus	Betula	Alnus	Quercus	Ulmus	Tilia	Corylus
3	14	47	25	3	9	118

This corresponds closely with the pollen composition at 80 cm., in the series from site *a*, and here too the sample contained remains of *Sphagnum* plants, both spores and leaves, together with *Phragmites*.

Site c

Cm. below surface	Alnus	Betula	Quercus	Pinus	Taxus	Phragmites	Carex	Characeae	Sphagnum	Notes
45-55	Stem and root	Rhizome	.	.	<i>cymbifolium</i> Fairly frequent	.
55	.	.	.	Stool <i>in situ</i>
55-65	Stem	Frequent fruits	+	.	Fairly frequent	.
65	Fairly frequent	.
75	.	.	.	Stem	Fairly frequent	.
80	.	.	.	Trunk <i>in situ</i>
75-85	Wood ab fruits	Occasional fruit	.	.	.	+	Root	.	Very rare and much eroded	.
85-95	Stems and roots	.	.	.	5 sporophyll	+	.	.	Abundant in pockets	.
95-105	Wood	Fruit	.	.	.	+	.	.	Abundant in pockets	Leaves of <i>Salix</i> <i>cinerea</i> ?
105-115	Wood	Rhizome	Fruit	.	Absent	.
115	Rhizome	Fruit	.	Absent	Loose, brown silty peat with much Phragmites
125	Rhizome and stem	Fruit	Very abundant	+	
135	Trunk <i>in situ</i>	
145	Twigs and fruit	.	Leaves	.	.	Rhizome and stem	Root and fruit	.	Absent	.
165	Wood	Rhizome	.	.	Absent	.
Clay	Rhizome

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Site *j* marks the approximate position from which were dug out the charred stumps of pines referred to on page 525. Pollen analysis of peat attached to the extracted roots gave the following results:

Pinus	Betula	Alnus	Quercus	Ulmus	Tilia	Corylus
33	23	40	3	0	1	27

Some *Sphagnum* spores were also present.

(2) *Outlying sites.*

A particular interest attaches to the examination of the western margin of Wood Fen, since in this direction the peat section is split into an upper and a lower portion by the occurrence of the soft clay known as fen-clay, or the "blue buttery clay". Analyses of Foraminifera by Dr MacFadyen, and rather scattered discoveries of the remains of large marine animals, such as whales, seals, etc., show this clay to have been a estuarine deposit. It occurs in this relationship to an upper and a lower peat very consistently over the whole of the southern part of the fen basin, so that many geologists have taken it as a constant stratigraphical sequence. As Skertchley pointed out, however, this relationship does not hold in the parts of fenland lying nearer to the sea, where peat and clay or silt beds replace one another in a very bewildering manner. At St German's a deep section showed no less than four peat beds alternating with brackish water clays. Even bearing this in mind, it would nevertheless prove of value if it were possible to date the formation of such a widespread and characteristic deposit as the southern fen-clay in terms of the forest and fen-sequence at the centre of Wood Fen. A tentative correlation has already been suggested, and examination of the outlying sites of Wood Fen where the fen-clay gradually tapers out, might be expected to confirm or refute this.

The most interesting site of this character is *d*, where the section is as follows:

	cm.
Peat disturbed by cultivation	0- 35
Peat relatively undisturbed	35- 45
Fen-clay with prostrate oak trunk in middle ...	45-105
Marsh peat with <i>Phragmites</i>	105-120
Hard basal clay	120 →

The lower peat is the foetid clayey peat known to the fenmen as "bear's muck". Three samples were analysed from the undisturbed part of the upper peat and one sample from the lower. The tree pollen results are given in Fig. 8, the non-tree pollen and spores in Fig. 7, and the other micro-fossils in the sub-joined table.

	Alnus wood	Quercus wood	Unidentified wood	Taxus male sporophylls	Juncus seeds	Chara fruits
35 cm.	.	.	+	.	.	+
40 "
45 "	.	.	.	+	.	.
Fen clay						
120 cm.	+	?	.	.	+	.

There appear to be no tree stumps in the peat here, and the content of tree pollen was probably derived therefore from the neighbouring fen woods. The transition from 45 to 35 cm. shows very striking changes in the tree pollen composition: pine and birch pollen increase very sharply to the top, oak pollen diminishes greatly and alder pollen increases; hazel pollen decreases throughout

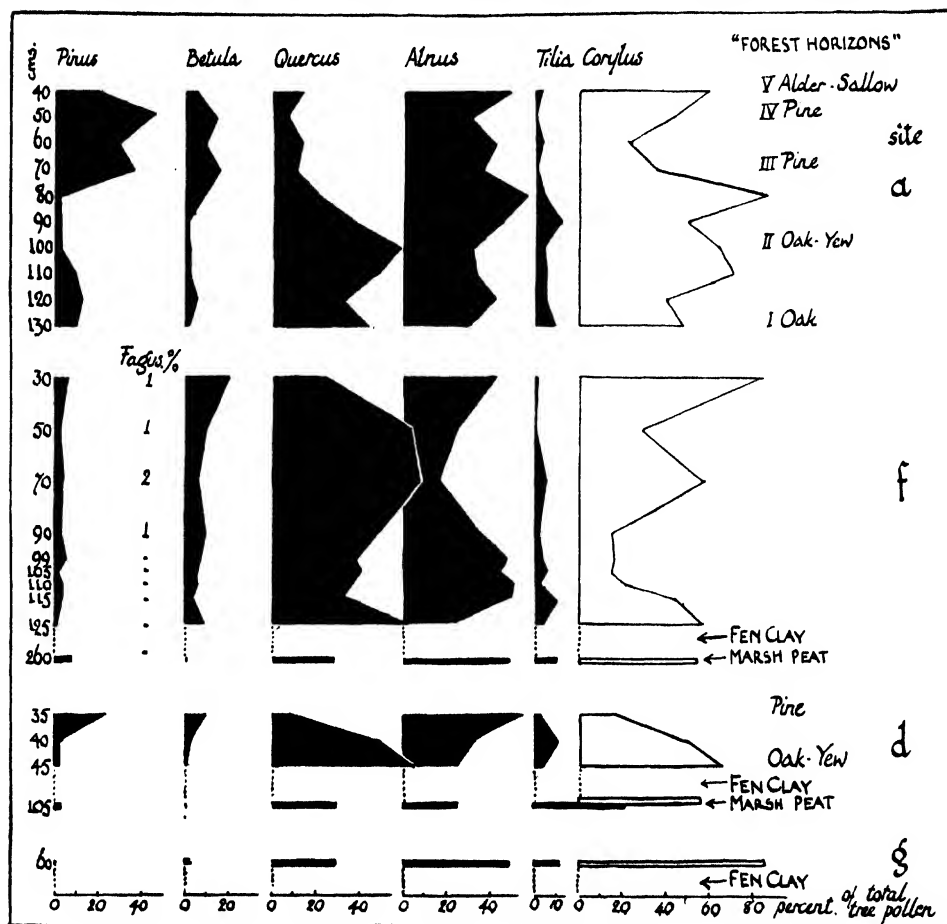


Fig. 8. Tree pollen analyses for *a*, *f*, *d* and *g*. These are set out together to allow easy comparison with a view to establishing whereabouts in the *a* series should be placed the period of deposition of fen-clay shown as present in sites *f*, *d* and *g*.

and lime shows a maximum of 11 per cent. at 40 cm. As will be seen from Fig. 8, these features strongly suggest correlation of 50-35 cm. in site *d*, with 100-75 cm. in site *a*. The hazel pollen alone possibly differs in the two diagrams. This would suggest the surface of the fen clay at *d* to correspond with about 100 cm. in site *a*, which is near the presumed oak-yew horizon. It is of interest that the micro-fossils show male sporophylls of yew in the 45 cm. sample from site *d*. The non-tree pollen neither strongly assists nor hinders the correlation,

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and this might indeed be expected since they are so much more local in their indications than the tree pollen. Nevertheless the *Chenopod*-type pollen, grass-type and aquatic type pollen are in general agreement with the suggested correlation.

The 100 cm. level in site *a* is about -4.4 ft. o.d., and the 50 cm. level in site *d* is -3.00 ft. o.d., so that here also the agreement is sufficiently close for the suggested correlation to have been possible, though this implies that there has been more subsequent compression of the lower peat layers at *a* than in the fen clay at *d*.

Passing further from the centre of Wood Fen the difficulties of correlation become much greater. The section at site *f* close to the Black Bank railway station shows 125 cm. of peat overlying 135 cm. of fen clay, below which again is a layer of foetid marsh peat. The tree pollen analyses for these peats are given in Fig. 8. It is, however, impossible to correlate them certainly with the results from site *a*; they may indeed correspond to a period not included in the *a* series. It is, however, possible to parallel the whole upper peat at *f* (from 125 to 30 cm.) with that part of *a* between 130 and 80 cm. (note that the vertical scales are different). If this holds, the formation of fen-clay at *f* must have begun and finished before it ever reached site *d*. The levels (Fig. 3) suggest also that this may have been so, but it is evident that the problem of this correlation must await much fuller investigation, especially into the conditions under which the fen clays were laid down. The presence of a small, but constant percentage of beech pollen in the top samples of the peat at site *f* may help to date the peat when our knowledge of the distribution of beech pollen in fen peats has widened.

Site *g*, chosen to be intermediate between *d* and *f*, gave peat samples practically devoid of tree pollen. The sequence was:

Surface peat	0-65 cm.
Fen clay	65-240 cm.
Foetid marsh peat	240-245 cm.

The analysis of the lowest sample of the upper peat is given in Fig. 8, but has no very great indicator value.

Two last sites may be mentioned. Site *k* lies at the North of Blackbank Drove and is a site where large subfossil yew trees are found rooted in the weathered Jurassic clay below a thin layer of peat now cultivated almost to the base. The base of the peat gave the following tree-pollen analysis:

Pinus	Betula	Alnus	Quercus	Ulmus	Tilia	Corylus
0	1	71	21	3	3	23

This evidently corresponds with the pre-pine phase of Wood Fen *a*, and it is possible that at the same time as the buried oak-yew horizon was growing in Wood Fen, these larger yews were flourishing on the fen margins, soon, however, to be killed and then preserved by the rising peat level during the

submergence which gave the fen clay at *d* and the aquatic pollen maximum at *a*.

Site *e* must be mentioned because of its archaeological interest. It marks the place where a fine Middle Bronze-Age spear head was discovered resting upon sand below the thin surface peat (see Fig. 3). Pollen analysis was not possible on account of the disturbed nature of the peat, but the site was carefully levelled and the spear horizon was found to be approximately -1.0 ft. o.d. Probability is in favour of the spear head having been covered up by peat soon after it was lost, and if so the peat which covered it is roughly of the same date as the spear. Since we know the level of the spear we can judge what depth of peat must have formed at site *a* in Wood Fen by the time the rising water-level caused peat first to reach the spear site. If we allow that the peat at site *a* has now become compressed to about 50 per cent. of its former thickness, then the pine phase of site *a* corresponds to the level of the spear site and might be supposed to be of Middle Bronze Age date.

DATING.

It is not proposed to enter into detailed comments on the possible age of the Wood Fen peats. The problem of the chronology of the Fenland peats should properly be considered only after the closest co-ordination of results from archaeological, historical, geological, botanical and other investigations. Through the efforts of the Fenland Research Committee this evidence is growing, but is still far from complete. In respect of the purely botanical evidence it may be pointed out that in Burnt Fen the Boreal pine maximum has been very clearly established in the lower part of a thick peat bed which *underlies* a thickness of some feet of fen clay (12). It is therefore practically certain, taken with the tree-pollen composition itself, that the Wood Fen pine forests are considerably post-Boreal in age. Pine forests of this later date are known both from stub horizons and from pollen analysis to have occurred quite widely in Fenland. Evidence of their exact age is not generally available although the upper submerged forest on the Lincolnshire coast at Ingoldmells, which contains abundant pine pollen (13), has been shown by Prof. Swinnerton to be associated with a Halstatt (early Iron Age) salt-making industry (14), and a site at Nordelph has yielded pollen analyses with a pine maximum well developed in peat underneath an extinct river which was flowing in Roman times (15). These facts do not disagree with the local evidence at Wood Fen that the pine forests may be of Middle Bronze Age. We may also note that a secondary (post-Boreal) pine maximum has been described in Denmark, Sweden and the British Isles as occurring in the sub-Boreal period—i.e. roughly, the Bronze Age—and this period in the same countries is quoted by Woodhead as showing a *Taxus* maximum (16).

These facts all have an obvious value, but a great deal of caution must be exercised before accepting the suggested Bronze Age date for these pine forests,

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and before correlating these with pine forests in other parts of the Fenland, of the British Isles or of Europe.

The need for such caution will be evident if we examine in detail the precise validity of the pollen analysis method as a means of establishing horizons of contemporaneity through the fen peats. In its simplest form the method reflects the catch made by treeless acid bogs of the pollen from the woodlands of the general upland soil of the countryside. Under these conditions the woodland composition is influenced directly by climate, the bog flora plays little part in influencing the tree pollen, and climatic changes are reflected over a wide area in changes of forest composition, which is in turn faithfully indicated by changes in the tree-pollen composition in the growing peat of the bogs. Under these conditions the general climatic change is a constant time horizon traceable over extremely wide areas in the changes of tree-pollen composition, especially when allowance has been made for the effects of altitudinal and of local climatic circumstances and possibly in some circumstances for the varying rates of dispersal of different species.

With lowland bogs of the "Niedermoor" type which occupy the English Fenland the position is much complicated by the fact that the bogs, at a certain stage of development, naturally become clothed with woody vegetation, firstly of the "carr" type dominated by *Alnus*, *Salix* and *Betula*, and later by "Zwischenmoorwald" dominated by *Quercus* or *Pinus*. The trees of these communities play an extremely important role in the pollen rain incorporated in the peat forming below them and in the bogs of the neighbourhood, so that the distant tree-pollen rain of the country outside the fens may be reduced to an insignificant proportion of the whole. These local fen woods are then liable to be major factors in the fen-pollen-diagrams, and it becomes important to examine the causes controlling their appearance, duration and extent. Fen woods arise by building up of the peat above water-level and therefore soonest appear in regions where the water is shallowest or the peat least water-logged, and may indeed be readily observed to extend out as a fringe from the edge of a fen towards the open water of a lake or broad. Under constant water-level conditions their extent will increase with time. The fenland, however, is in a region of very low rainfall and its peat is dependent on an external supply of drainage water: increasing rainfall making for increased flooding of the fens would restrict the rate of spread of the fen woods or might even cause retrogression, decreasing rainfall would have the opposite effect. We cannot say with certainty how far the rainfall factor may have altered in the past, but it is quite certain that another factor of similar effect has repeatedly occurred. This is the alteration in the relative levels of land and sea. Land subsidence, by causing marine flooding or at least backing up of fresh water, and by lowering the drainage gradient would, as we have shown at Wood Fen, interrupt the growth of the fen woods by a return of open water or reed-swamp conditions. Relative elevation would, on the other hand, cause better

drainage and hasten the acidification of surface peat and the spread of the fen woods.

Many fen pollen diagrams show as major features changes in the relative amounts of hygrophilous trees such as *Alnus* on the one hand, and more mesophytic trees such as *Pinus* and *Quercus* on the other.

These changes may evidently be related either to local or to general changes in the status of the fen woods, and the incidence of the pine or oak in two diagrams from widely separated sites may not therefore indicate a similar age in the two cases. Nevertheless a cycle indicative of change from wet to dry conditions and back, of spread and then retrogression of fen woods, may be taken as generally synchronous in separated fen sites, for such an effect will most likely be due to a general change either of climate or sea-level, and either will serve as a time horizon for the fens. Though fen woods may originate and persist locally at diverse times, yet there will tend to be well marked major periods of extensive fen woods which should be recognisable both as buried forests and in correlated pollen diagrams.

Over and above these effects on the *extent* of the fen woods, there is to be considered the effect of climate on the composition both of the mature fen woods and of the forests of the drained fen islands and fen margin. Thus we appear to find the fen woods of one period dominated by *Quercus*, and of another by *Pinus*. Similarly *Taxus* is not found in all levels of buried fen forests, and the pollen of *Carpinus* and *Fagus* is limited to the upper peat layers. These indications appear to be utilisable for chronological horizons in the peat succession.

We may conclude that the pollen-analysis method has a valuable general applicability to the problem of establishing fen chronology, but that extreme care is needed for the detailed correlation of sites, which ought not to be decided without consideration of the development of the bog as indicated by all aspects of its fossil content and by the local topography.

SUMMARY.

1. The investigation deals with the post-Glacial deposits in Wood Fen 3 miles north of Ely.

2. Evidence is given that in the last 200–300 years artificial drainage has caused the surface level of the peat to fall by about 10 ft. Reasons are given for regarding this as due rather to surface peat wastage than to shrinkage or compression.

3. The sequence given by Skertchley for the buried forests present in the Wood Fen peat is set out, discussed and confirmed. From the base there are, in order: (1) oak, (2) oak-yew, (3) pine, (4) pine, (5) alder-willow-sallow.

4. In the centre of Wood Fen the results of tree-pollen analysis are shown to conform to the forest sequence. Non-tree pollen and other micro-fossils are used as indices to the past development of the fen. Particularly striking is the

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abundance of remains of *Sphagna* and it is suggested that the Wood Fen forests have the character of "Zwischenmoorwälder". Evidence is produced for the development of such acidic peats above alkaline topogenous peat both in the Norfolk Broads and in Fenland.

5. It is suggested that the development of the peats of the middle of Wood Fen agrees with a sequence of conditions: (1) of stability or elevation, (2) of submergence (coinciding in the neighbouring fens with deposition of semi-marine clay), (3) of stability or re-elevation, (4) of subsidence (or possibly increased rainfall). Since the formation of these buried forests there has probably been a net downward movement of land relative to sea-level of about 15 ft. or more.

6. Peat analyses are described for the marginal sites of Wood Fen with a view to establishing geological and archaeological correlations. The pine forests are established as clearly post-Boreal in age, and possibly to be correlated with the Bronze Age.

7. The value of the pollen-analytic method for correlation of the fen peats is shown to be bound up with the recognition that local fen woods greatly influence the form of local pollen-diagrams, so that it becomes essential to work out the phases of bog formation and development for each area investigated, and to interpret the pollen diagrams in the light of these results.

8. It is essential to realise that fen development may be controlled by three major factors acting either singly or together. These are (1) the natural processes of vegetational succession, (2) edaphic and topographic effects such as those produced by relative movements of land and sea and (3) climatic change, especially perhaps in regard to temperature and rainfall. The history of fenland development can only be satisfactorily developed, whatever technical methods are employed, by analysis in terms of the operation of these causative factors.

The authors desire to thank Major G. Fowler, who kindly supplied the history of the drainage of Wood Fen, and Mr Fryer, who informed us of the records of *Trichoptilus paludum* from Wicken Fen. In particular we are grateful for the critical and friendly advice of Prof. A. C. Seward, F.R.S., Prof. A. G. Tansley, F.R.S., and Prof. O. T. Jones, F.R.S., and for the kindness of Mr Mitcham in allowing us ready access to his land.

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SOME PRACTICAL POINTS REGARDING THE DETAILED BOTANICAL ANALYSIS OF GRASS-VELD OR OTHER PASTURES BY THE LIST QUADRAT METHOD

BY S. M. MURRAY, B.A. (CANTAB.), M.Sc. (RAND), AND P. GLOVER.

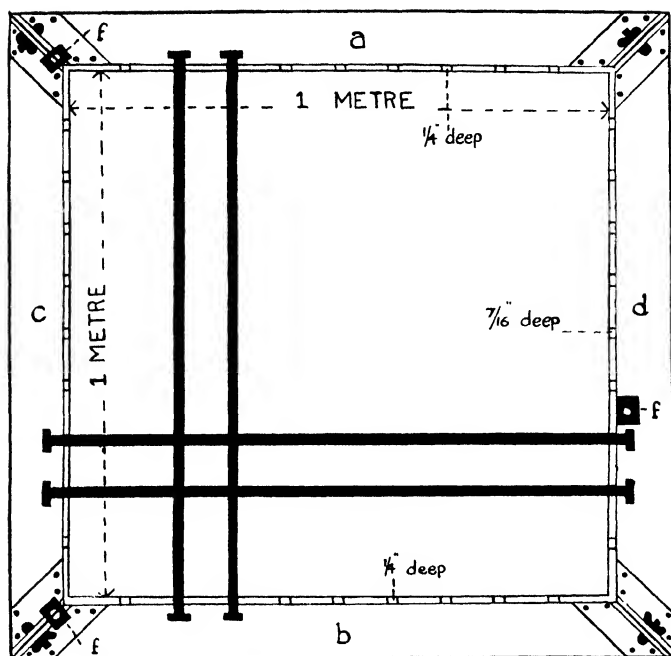
(*Botanical Department, University of the Witwatersrand, Johannesburg.*)

(*With one Figure in the Text.*)

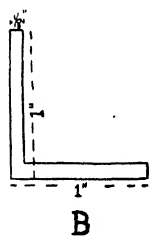
WHATEVER method is decided upon for the botanical analysis of veld, it is in most cases necessary to modify that method to suit the particular type of community to be studied. Furthermore, a number of practical difficulties have to be overcome as the work progresses. It is proposed, therefore, to describe in detail the procedure adopted for the study of the botanical composition of natural veld, by the list quadrat method, in certain grazing and fertilising experiments recently laid down at the botanical research station of the University of the Witwatersrand.

The areas in question consist of a number of 2-acre camps enclosing for the most part *Tristachya Rehmannii*—*Elyonurus argenteus*—other spp. grass veld which is typical of large areas of this part of the High Veld just north of Johannesburg. A primary survey of each camp was first made in order to make it possible to select sites for the quadrats in such a way that variations in the cover and important plant communities were represented jointly. It was found that by carefully selecting the sites for ten permanent quadrats, areas representative of a camp could be obtained.

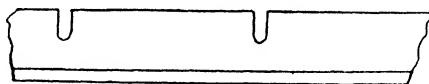
The apparatus required for the detailed analysis is a quadrat frame designed to enclose one square metre and divisible into 100 decimetre squares. Since the analysis of these camps was carried out, a frame which is a decided improvement upon the original has been developed and is now being used. This frame consists of four lengths of $\frac{1}{8} \times 1$ in. angle section iron (Diagram B). Aluminium was first tried, but proved unsatisfactory on account of a tendency to warp, and a lack of rigidity. The frame is cut in such a way that when resting on the ground the upright arm of the L is exactly 1 metre in length, and the horizontal section, instead of being square at the ends, is cut to make an angle of 135° (Diagram A). Angle pieces are then rivetted to this arm with the upright sections fitting flush with the 135° angle. Of these one is fitted horizontally with a bolt and wing nut and the other slotted to fit a similar bolt (Diagram D). Thus, when the four lengths are bolted together as in Diagram A, a perfectly rigid square frame with an inside measurement of 1×1 m. results. Along the upright edges of each side of the frame are ten slots 1 decimetre apart (Diagram C) cut



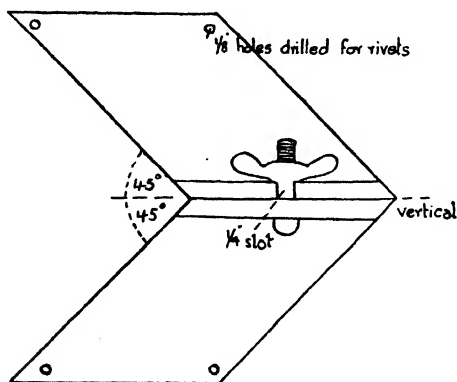
A



B



C



D

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to accommodate $\frac{3}{16}$ in. diameter rods. Sides *A* and *B* (Diagram A) are slotted to a depth of $\frac{3}{16}$ in., while sides *C* and *D* are slotted to a depth of $\frac{3}{8}$ in., to allow the rods fitting into sides *A* and *B* to overlie those fitting into *C* and *D*. At the end of each rod, which is just over 1 m. in length, brass collars are fitted to prevent them slipping through the slots. Four of these rods are required, so that by moving them to the desired slots a decimetre square of the quadrat can be analysed at a time. The fittings *F* (Diagram A) are sockets made to fit a camera tripod specially designed for photographing the quadrat in plan before listing.

This frame has the advantage of being easily assembled and portable when taken apart, which makes it a great improvement on the folding wooden frame that was used previously. This pattern frame, complete with its golf-bag pattern case facilitating transport, can be made in Johannesburg for approximately £3, and probably less in Britain.

With a frame of this type the detailed botanical analysis of each selected site was made in the following manner. In each decimetre square, estimations were made of the percentage of ground covered by the various species present, and entered in the corresponding square of a blank diagram of the quadrat together with the total percentage cover of all the species occurring in the square. The estimations were all made at ground level, thereby giving the basal cover, and in order to assist in judging this, a small movable frame was used which divided each decimetre square into twenty-five equal parts so that one of these subdivisions represented 4 per cent. of the area. This frame was soon discarded however when sufficient experience had been gained in judging the cover by eye.

Besides making the entries described, the percentage cover of each species was also entered under the name of that species on a separate sheet, so that the totals could readily be worked out for the whole quadrat. This means making two entries in the field for each estimation, but the time saved in making the final calculations is considerable. It was also possible, by adding up the total covers recorded in each square of the diagram and comparing this with the same result arrived at by adding up the total percentage cover of each species, to check the accuracy of the entries and calculations.

A further sheet was then drawn up upon which the names of all the species were entered, with the percentage cover of each worked out and expressed as a percentage of the total cover—not the total area of the quadrat.

The data thus recorded give all the necessary information, in terms of density and distribution, for each quadrat. The squared diagram gives the distribution of the species with almost the same accuracy as a chart, and the entries on the second sheet largely facilitate the working out of the percentages of each species which are shown on the third sheet. By averaging up the results of the 10 or more quadrats in a camp, a very fair idea of the botanical make up of the whole area is obtained.

Since the quadrats are permanent and will be re-listed in the future, they were marked at the corners with small metal pegs and also labelled with a stamped metal label. In order to mark the sites a dropper was driven in some 3-4 yards off—this being a sufficient distance to prevent cattle, which were attracted by these droppers, from trampling the sites unduly.

NOTES ON TECHNIQUE.

In considering such a detailed and apparently laborious method of pasture analysis, one might be led to suppose that the time taken to list one quadrat would limit the number that it would be possible to complete to such an extent as to cause inaccuracy. It was found however that by careful organisation, two workers could complete 8-10 quadrats in a working day of 8 hours.

In early stages of the work, much time was occupied in identification of the species. The variation and the appearance of the grasses at different times of the year and under varying weather conditions make identification all the more difficult at the outset; and habitat, colour, appearance of the root stock, type of leaf, and taste, besides the flower head, have to be relied upon collectively for identification. However, after completing one or two quadrats in typical veld, identification of species ceases to be a difficulty except in a few isolated cases. Estimation of the cover can soon be judged quickly and with sufficient accuracy, for an error of one unit in a decimetre square means an error of 0.01 of a unit only in the whole quadrat.

With the method of listing employed, it is essential for practical purposes that two observers work together on one quadrat, each spending part of the time recording while the other identifies the species and estimates the cover. With careful distribution of labour, especially to save time between the completion of one quadrat and the selection of a site for the next, it was found possible to average at least one quadrat per hour throughout the day's work in the field. This means listing the quadrat at the rate of about 2 decimetre squares per minute.

ACKNOWLEDGMENTS.

The writers wish to express their thanks to Dr John Phillips, Professor of Botany of the University of the Witwatersrand, for suggesting the method of analysis and type of apparatus, to Mr J. D. Scott who, with the senior author, carried out the earlier botanical analyses and was largely responsible for working out the details of this method, and also to Mr A. Griffiths, who, with the advice of the junior writer, constructed and assisted in the designing of the new pattern quadrat frame described.

REVIEWS

THE MAY ISSUE OF *THE JOURNAL OF ANIMAL ECOLOGY*

(VOL. 4, No. 1, MAY 1935)

THE present number contains 16 papers, 2 notes, 8 reviews, and 107 short notices of British publications on animal ecology. The latter are issued in duplicate in a form suitable for use on index cards, and can also be obtained separately from the *Journal* for 3s. 6d. per annum.

The direct influence of the physical environment on animals is treated by D. M. Reid, in a paper on the intertidal distribution of a sea-urchin in relation to the North Atlantic Drift. G. C. L. Bertram shows, from experiments conducted in East Greenland, that Arctic insects and spiders have lower activity limits and optima for temperature than those of temperate regions. A carefully controlled experimental study of the South American blood-sucking bug, *Rhodnius prolixus*, is described by Nancy Clark, who has defined the effects of temperature and humidity on the eggs.

Habitat surveys also receive attention: a quantitative analysis of the fauna of a Yorkshire chalk stream by H. Whitehead, for comparison with previous studies published in the *Journal of Ecology*; habitat observations on rooks, lapwings, and starlings, made from the train by B. J. Marples; and a summary of a number of surveys organised by C. Elton through the medium of a broadcast, designed to show the types of woodland bird communities in England. It is shown that woodland birds form a very distinct, ancient, and widespread community.

B. M. Hobby contributes a large report giving records of 498 preys taken by Asilid flies in a locality in Southern Rhodesia.

There are a number of population studies. A census study of badgers in south Shropshire by Frances Pitt proves that these animals have increased greatly since 1900. John Ford gives some notes on mole density on pasture land. There are two ant studies: Walter Pickles, in a survey of the nest colonies of three species of ants in Yorkshire, describes how the ants live, their non-hostile interrelations, and some figures for nest populations. Cyril Diver publishes a map of some wood-ant colonies in Scotland, showing nest territories.

Bird population studies include a census of short-eared owls in an area on the Scottish Border, by T. Russell Goddard; the results of a number of census counts of heathland birds by D. Lack and other observers, together with a special account of Skokholm birds over seven years by R. M. Lockley; and a statement, backed by census figures, of the state of the partridge population in England in 1934, by A. D. Middleton.

Fluctuations in populations were studied by H. F. Barnes in some work on the *Arabis* midge and its parasites; and by J. G. Myers, who describes the remarkable periodic epidemics which occur among reptiles and fishes in the Orinoco River.

There are two notes on introduced animals: the introduction of lizards (*Lacerta viridis*) on to the coast of North Wales, by S. Zuckerman; and of some recorded escapes of coypus (nutrias) from fur farms, by T. Warwick.

There are reviews of the *Journal of Ecology*, the mathematical and biological studies of Lotka and Severtzoff on animal populations, work on partridges introduced into America, of a text-book on plant ecology, a book on Lancashire birds, a study of the relation of herring movements to the presence of diatoms and colonial flagellates, and a book on bird psychology. The Notices cover all important British work published during the period.

CHARLES ELTON.

Praeger, Robert Lloyd. *The Botanist in Ireland.* With 6 coloured maps, 44 plates and 29 figures in the text. Hodges, Figgis and Co., Dublin. Price 12s. 6d. 1934.

This is an unusual kind of book. It consists of four main sections: first an account of the geological history, topography and climate of Ireland; secondly a "botanical description" including a history of the flora, a discussion of the "Atlantic flora", a comparison of the British and Irish floras, brief accounts of the principal types of vegetation, notes on the botanical subdivisions of the country that have been made, a list of the chief writers on the Irish flora with notices of their discoveries and publications, a list of "rare or interesting plants" with descriptive and critical comments; thirdly (occupying the greater part of the book) a detailed topographical and botanical description of the whole country according to a definite sequence of areas chosen for their natural unity as plant habitats; fourthly a "census list" of Irish plants, giving the numbers of the vice-counties in which the species occur.

It goes without saying that, with such a programme, a botanist of Dr Lloyd Praeger's unrivalled knowledge of the Irish flora based on a continuous record of indefatigable field work and careful study of the results, added to his critical acumen, sound sense and scholarly mind, could not fail to produce a work packed with every kind of information interesting and useful alike to taxonomist, plant geographer, and lover of nature. The book is scarcely one to read straight through, but it is fascinating to dip into, and will be invaluable as a work of reference. Its contents are far too varied to comment upon in detail: it need only be said that the general portions give an extremely vivid conspectus of the conditions and nature of the Irish flora, the special parts most interesting and judicious estimates of the status of individual species and of the nature of their habitats, and that almost every page raises unsolved problems and stimulates various questionings in the mind of the reader. One may regret, however, that Dr Praeger did not include some more description of the vegetation, as distinct from the flora, of the various localities he deals with. Besides his own excellent publication, in conjunction with Dr Pethybridge, of the district south of Dublin, now more than 30 years old, his somewhat later account of Clare Island, and a very few isolated pieces of more recent work by others, we have very little material from which to form a picture of the natural vegetation of Ireland as a whole.

A somewhat novel plan of numbering the contents has been adopted. There are no page numbers (except in the census list and index) but in place of these there appear at the top corners of the pages the numbers of the paragraphs, each dealing with a particular topic or species, into which the text is divided. On a rough estimate the book actually contains about 600 pages. The maps, plates and figures add greatly to its value.

We hope this work will lead, as it should, to an increased number of visits of British botanists to Ireland and to a more widely diffused and more intimate knowledge of the flora and vegetation of that most attractive island.

A. G. TANSLEY.

Corbet, A. Steven. *Biological Processes in Tropical Soils with special reference to Malaysia.* Pp. xiv + 156, with 10 text-figures and 7 photographs. Heffer and Sons, Cambridge, 1935.

The author of this little book, who was at one time bacteriologist at the Rubber Research Institute of Malaya, gives an interesting general view of the chemical and biological processes in Malayan soils. He shows that in the untouched rain forest dynamic equilibrium is maintained under the remarkably constant conditions of temperature and moisture. When forest is cleared and the soil exposed it is well known that the nitrogen content falls, but this cannot be explained, as has been assumed, by an increase of micro-organisms resulting from

the higher temperatures and causing decomposition of the nitrogenous substances, nor by mechanical removal in erosion. "Almost the only possibility left is that increased insolation is responsible for a photochemical change which results in humic matter being broken down to carbon dioxide and nitrogen, together with smaller quantities of ammonia and nitrate, and experimental evidence has been adduced which shows that this explanation is almost certainly the correct one... The precise nature of this chemical mechanism... is obscure." The implication is in favour of the so-called "forestry method" of rubber growing, in which a natural ground cover is allowed to establish itself so that humus and nitrogen increase and an approximation to the old equilibrium of the natural forest is re-established. A serious objection to this procedure is, however, the probable harbouring by the natural cover of a population of small mammals which are carriers of serious human diseases. The extreme complexity of the factors at work and the difficulty of re-establishing a new equilibrium compatible with human requirements once the natural equilibrium has been destroyed are very apparent.

The author touches on a great number of important ecological topics, far too numerous to notice here. The account of the general conditions of life in Malaysia is well done and informative, but the publishers claim that the book will be "intelligible to the planter and agriculturalist", is hardly justified, as regards considerable portions at least. The photographs are extremely good and well chosen and admirably illustrate the various aspects of Malayan vegetation, both natural and artificial, but the screen employed in their reproduction is too coarse and this rather seriously detracts from their appearance. A. G. T.

Kirkpatrick, T. W. *The Climate and Eco-climates of Coffee Plantations.*

Pp. 1-66 with 34 tables and 34 graphs. The Crown Agents for the Colonies, 4 Millbank, London, S.W. 1. Price 5s. 1935.

The author, who is an economic entomologist, has carried out a careful study, lasting for the greater part of a year, of the "eco-climate" of a coffee plantation at Kiambu near Nairobi in Kenya Colony, at an altitude of 5650 ft. (1722 m.). The "standard climate" of this station, though close to the equator, is, as the author remarks, much more truly "temperate" than that of much of the so-called "temperate regions", being very equable, without extremes of drought and rainfall or of temperature. The author states that eco-climates occur in close proximity "which differ as widely from the standard as the standard climates of London, Khartoum and Mombasa are from each other". The coffee plantation, with hemispherical bushes about 7 ft. high and planted 8 ft. apart, always showed a greater range of temperature than the standard screened thermometers. The differences varied from a fraction of a degree to 6.2° C. at different times of day and night and under different weather conditions. The humidity of the air also showed a greater range. At night it is cooler and damper in the plantation than in the screen, though only very slightly on heavily overcast nights. By day it is generally warmer and drier, though with a cloudy sky it may be warmer and damper. The evaporation in the plantation is on the whole much lower than in the screen, for it is only on the hottest and driest days that the increased temperature and saturation deficit compensate for the great reduction of wind in the plantation. The reason for the higher day temperatures in the plantation appears to be that most of the insolation is reflected from the leaves and warms the air close to the bushes by conduction and convection, while the reduction of wind checks the removal of this warm air. Similarly at night the hemispherical crowns of foliage will lose more heat by radiation than would be lost from the earth, just as they receive more during the day. Though differing so markedly from the standard climate, the eco-climate shows a definite correlation with it, as is clear from the author's numerous graphs, and it is possible to deduce with a fair degree of accuracy the conditions in a close-planted unshaded coffee plantation on level ground.

Mr Kirkpatrick's work contains many data of value for the ecologist which cannot be dealt with in a short notice. It is interesting to note that his observations on the temperatures of coffee leaves agree fairly well with A. M. Smith's results in Ceylon. About noon on a day with bright sun during the warm season the temperature of a fully exposed leaf is likely to be between 35° and 45° and usually 10–15° above the air temperature. The light inside a thick bush may be as little as 1·2 per cent. of that in the open.

This paper is an excellent example of thorough and really scientific study of a particular ecological problem. It is only through work of this type that the scientific foundations can be laid on which really efficient forestry, horticultural and agricultural practice in the widest sense can be built, and it is to be hoped that the colonial governments are now at last beginning to recognise the fact.

In subsequent communications it is intended to deal with the influence of different eco-climates on the insect populations of coffee plantations with particular reference to species of economic importance, and with the extent to which the numbers of a species can be regulated by deliberate modification of the eco-climate of its habitat. A. G. T.

THE ORIGIN OF MEDITERRANEAN VEGETATION

Markgraf, Fr. Genetische Berichtungen der Mittelmeerflora. *Ber. d. deutschen bot. Gesellsch.* 52, 68–79. 1934.

Dickinson, Olive. Les espèces survivantes tertiaires du Bas-Languedoc. *Station Int. de Géobotanique Méditerranéenne et Alpine*, Comm. 31. Montpellier, pp. 1–157. 1934.

Dr Markgraf distinguishes *genetic elements*—groups of species which have identical geographical relations and are thus inferred to be of equivalent origin—from *floristic elements* which have the same general existing distribution. Thus species whose main distribution is round the Mediterranean basin, but actually occur also in the British Isles, form the Mediterranean *floristic element* in the British flora. But these may represent several different *genetic elements* within the Mediterranean flora itself. The disentanglement of such genetic elements in a flora is not always easy, but when it can be done on good grounds the results form a very valuable contribution to the history of the changes in the flora of a region.

Species which occur in the Mediterranean mountain forests frequently extend through the damp woods of Central Europe far to the northward. Others which have their homes in the warm dry eastern Mediterranean peninsulas may extend without a break into the steppes of southern Russia and as far as western Siberia, or even to the steppes and semi-deserts of Central Asia. But more interesting are species whose closest allies belong to more distant countries with wide intervening regions from which the generic stocks are absent. Thus *Gladiolus* spp. and *Erica arborea* have the great mass of their congeners in South Africa, with a few connecting links on intervening African mountains. More striking still is the entirely isolated *Pelargonium Endlicherianum* in Syria and Cilicia, and three species of shrubby *Violas* in southern Spain, northern Albania and Macedonia. All these form the scanty remains of an old Mediterranean element that is represented now by few species, ecologically very various, and must have come from the Cape after the disappearance of the Sahara Sea, probably in the Pliocene when what is now the Algerian Sahara became a land surface. *Caralluma europaea* and *Chamaerops humilis*, on the other hand, belong to an old Palaeotropical element with allies right across Africa into the Indian desert in the former, and in India and eastern Asia in the latter case. This tropical genetic element may have been much more numerous in the Mediterranean basin during the Tertiary, when the climate was much damper: only species which could stand the increasing dryness have been able to survive there. Another genetic

element, adjusted to cooler climates, is represented by *Pinus peuce* in the Balkans, which is closely allied only to *P. excelsa* in the Himalaya and more remotely to the other species (East Asiatic and North American) of the section *Strobus*. To this element belong also the north Mediterranean *P. nigra* and the very closely similar east Asiatic *P. thunbergii*: *Picea omorika* (Balkans) and *P. ajanensis* (Amur region): *Forsythia europaea* in north Albania, with all the other species in temperate eastern Asia: *Aesculus hippocastanum* in Albania and Epirus, with allies only in eastern Asia and North America; and many other stocks with similar discontinuous distributions. This *arcto-tertiary element* consists mainly of forest species, and thus we may infer a Tertiary tropical forest belt in the southern Mediterranean region and a subtropical belt to the north, extending to central Europe and even to Spitsbergen and Greenland, as the fossils show. This last included stocks which could bear cold (e.g. the ancestors of our common beech) but also others which required warmth, e.g. *Glyptostrobus*, now represented only by *G. pensilis* in tropical China. The discontinuity of the existing species must be attributed to climatic changes, such as the desiccation of south-eastern Asia after the retreat of the Siberian Sea, which has separated the arcto-tertiary Himalayan from the Mediterranean representatives, e.g. *Cedrus deodara* from *C. libanitica*, *Prunus acuminata* from *P. lauro-cerasus*—the last named again being separated by a sea barrier from *P. lusitanica* (Portugal and the Canaries).

Within the Mediterranean region itself the most striking difference is between the eastern and western basins. Thus *Ulex* has many species in the western and is quite absent from the eastern: *Cistus* has many more species in the western than in the eastern basin. On the other hand some stocks belong to the eastern half: e.g. *Acantholimon*, a cushion plant of dry peaks, and *Platanus orientalis*, inhabiting alluvial woods; while *Astragalus* sect. *Tragacantha* has many more species in the east than in the west. The eastern and western basins existed for a long time independently: only in the late Miocene and early Pliocene was land developed to connect the two basins: before that they were separated by sea. The species which are distributed round the entire Mediterranean are partly old, predating the separation, but partly (where the later land is involved) younger, occurring only after the later land connexions were established. The older type of distribution is seen in the occurrence of twin species, one in each half, e.g. *Cedrus libanitica*, *C. atlantica*: *Prunus lauro-cerasus*, *P. lusitanica*: *Ramondia serbica*, *R. pyrenaica*: *Rhododendron ponticum*, *R. baeticum* (south Spain and south Portugal). In the last case the "omni-mediterranean" original distribution is proved by the occurrence of fossil *R. ponticum* from Bulgaria (Pliocene), Macedonia (Miocene) and the Alps (Interglacial).

A careful study of the distribution of the species of the eastern and western groups shows that the line of separation between the two does not run north and south but east and west, from Asia Minor through Greece, south Italy and Sicily to North Africa. There was no land connexion where Central Italy now lies, and this is shown also by the geological evidence. On the other hand there was land, at least an archipelago, connecting southern Italy and Sicily with Tunis in Pliocene times. Besides this, in the Miocene, and perhaps into the Pliocene, there was "Tyrrhenis" connecting Tunis with Sardinia, Corsica and Tuscany, also with Liguria, and southwards with Sicily and Calabria—again a reconstruction borne out both by geological and distributional evidence.

Thus the existing flora carried by the narrow edge of the present sea together with the Mediterranean islands has very various origins, some of it going right back to the Tertiary flora which, in Central Europe, was destroyed by the ice of the Pleistocene and can only be reconstructed from fossils. The effect of the ice-age on the Mediterranean flora itself was very slight. This is shown already by its high mountain flora which contains more endemics than the Alps, endemics derived from the stocks of the neighbouring lowlands. Very few species are common to the Alps and the high Mediterranean mountains, and those only such as migrated from the Alps to the Arctic at the close of the ice-age (*Saxifraga oppositifolia*,

Silene acaulis). Doubtless their southern migration to the Mediterranean peaks does bear witness to a cooling of the Mediterranean climate in glacial times, permitting them to cross intervening country where now they are extinct. Post-glacial changes too seem to have been slight, so that the history of the older (pre-glacial) stocks is easier to trace than that of the more recent flora which has undergone much less change than that of central and northern Europe.

Dr Olive Dickinson has studied the surviving Tertiary flora of a small portion of the Mediterranean region—Bas-Languedoc. This was more strongly affected by the ice-age than most of the region by reason of its proximity to the Pyrenees and Auvergne from which glaciers descended, though they were far from reaching the mouth of the Rhone. The cold of the ice-age is witnessed by the remains of the mammoth and of the woolly rhinoceros in contemporary deposits, and by the disappearance of a number of thermophilous species of plants. Of the existing rare species of this district, excluding obviously recent invaders, the author considers 140 “eu-Mediterranean” species as survivals from a warmer (Tertiary) climate. These species are found in isolated colonies of discontinuous distribution, they often lack the means of easy dispersal, they occur mainly in the southern part of the district, on open soil, in rather remote places relatively free from the destructive activities of man and his animals, and with rare exceptions on pre-Quaternary deposits. All these characters of occurrence and habitat suggest survival *in situ* of the species in question, probably from the Pliocene, which had a climate closely similar to the existing one, but with more thermophilous species. A certain amount of shifting and migration has no doubt occurred among them favoured by climatic changes such as the inter-glacial, but the *ensemble* of the evidence is unmistakable.

A. G. T.

THE DISCONTENTS OF PHYTOSOCIOLOGY

Katz, N. J. Die Grundprobleme und die neue Richtung der Phytosoziologie. *Beiträge zur Biologie der Pflanzen*, 21, 133–66. Breslau. 1933.

Dr Katz is well known as one of the most active among the extremely energetic Russian plant sociologists, and readers of this *Journal* will be familiar with his excellent account of the Sphagnum bogs of central Russia published in 1926. In the paper under review he complains of the undue attention given by the Scandinavian workers to the statistical problems of the distribution of species in plant communities and to the theoretical problems connected therewith, and he deplors the neglect of what he considers the fundamental task of plant sociology—the clear delimitation of “associations”, which can only be attained by the unification of descriptive methods. Katz regards as illusory the attempts to define “minimal areas” and to establish laws of the “constancy” of species in associations, and his view is not without justification. We urgently require a critical investigation into what statistical theory can, and cannot, do in formulating the facts of species distribution in plant populations. Until we have such a treatment we shall make no real progress in that direction.

It is extremely unfortunate that the term “association” has become so widely attached among the eastern continental workers to the very small units which they regard as the fundamental units of vegetation. The term was never intended to apply to such units by its originator Humboldt, nor by those who tried, much later, to develop and define the concept. The Scandinavians, who are responsible for this unhappy transference, are now inclined to revert to a wider use, but the mischief has been done. Between Clements’s application of “association” to a very large unit and the Russians’ to a very small one there is every variation of usage, and the chaos is again nearly complete. It is a pity that the term “synusia”, first used in print by Gams in 1918, was not universally adopted for these small collections of ecologically allied species living in company which central and eastern Europeans

have got used to calling "associations" during the last 15 years. A minor but very real objection is that in its German form (the commonest in international use) the word has no less than six syllables (in the plural, seven), and since it is applied to a vast number of different objects it has to be used very frequently indeed in descriptions and discussions. The effect in spoken language is extremely distressing!

The psychology of the use of technical terms is not uninteresting. When a word of ill-defined connotation becomes, from any cause, fashionable, people come to use it either so loosely that it loses any value it may originally have had, or else for a particular concept (lying within the limits of the original loose denotation of the term) in which they are specially interested. A great number of writers on ecological subjects who are not interested in the theory of the constitution of vegetation or its terminology now use the term association for any collection of plants growing together to which, at the moment, they wish to refer. Serious students of the theory of vegetation use it for the particular unit they believe to be fundamental: Clements, who is accustomed to think in terms of vast continental formations, for the great aggregations of species which form the basis of the great climatic climaxes; the Russians, who study Sphagnum bogs and grasslands in minute detail, for the smallest (or almost the smallest) social units they can distinguish. Each thinks his own use is correct, because each thinks the unit in which his interest centres is fundamental. It is just the same with the term "species". From the old "aggregate species" we have passed to an almost infinite multiplicity of "micro-species", and it is only the inconvenient phenomenon of hybridism, with some hybrids which segregate and others which breed true, that prevents the extremists from insisting that the term species shall be applied to "pure lines" only. Impatient people then propose to abolish the term altogether, as Warming wished to do with "formation", and as Ronald Good has recently proposed with "species". There will never be agreement until it is generally recognised that you cannot shortly define a "species" or an "association" in the old sense, that the units met with in the field are ill-defined by their very nature; but that the terms may nevertheless be very useful if workers can agree on the approximate rank of the entities to which they will apply them. For new concepts, like that of the "micro-association", new terms must be devised. At the moment there is as little prospect of general agreement among plant sociologists as there is of political agreement in Europe, and for the same reason. Everyone is far too much obsessed with the exclusive importance of his own interests.

Dr Katz's paper contains a great deal of sound sense. After criticising effectively the statistical efforts of the Scandinavians and also the conception of "characteristic species" he concludes definitely for the decisive importance of dominants in any plant community. In this he is happily in agreement both with Clements and with Du Rietz's more recent views, and we cannot doubt that he is right. The dominants, Katz holds, can and should be used to give a short diagnosis of the community, each layer of vegetation being taken separately. The names of the dominants of each layer, beginning with the uppermost, should be joined by the sign +, while the successive layers are linked by the sign -. Some such system is now used by a number of workers in different countries.

The most important constructive contribution is the author's insistence on the necessity for studying the ecology of the individual species in order to obtain an insight into its capacity for association with other species. The "ecological amplitude" of a species explains its capacity for occurrence in a greater or smaller number of communities, and the ecology of a community is determined by its constituent, and mainly by its dominant, species. These considerations, which are undoubtedly sound, were put forward by Katz in 1926, and were also advanced in 1929 by Gams who said that a thorough study of the species was the only proper road to a knowledge of the association. In other words we must get back to "autecology" in its widest sense. All this should be self-evident.

Finally the author takes the common ling, *Calluna vulgaris*, and considers its ecology and

the plants with which it enters into association in the different parts of Europe. This predominantly west European species extends eastwards with decreasing frequency to the other side of the Urals. Its most widespread associations are said to be with *Pinus silvestris*, *Pleurozium (Hypnum) schreberi*, *Cladonia* spp., especially *C. silvatica* and *C. rangiferina*, *Sphagnum fuscum*, and some other species, and these are determined, according to Katz, by its oligotrophy and xerophily. After a brief and rather inadequate survey of recorded associates, he concludes that in western Europe *Calluna* occurs on open Atlantic heaths and oligotrophic moors in combination with *Sphagnum* spp., mainly *S. fuscum*: in Finland and the Russian coasts of the Baltic and White Sea it is found on moors with the same species, but on mineral soil in pinewood; while in eastern Europe it occurs only in semi-natural woods which have been disturbed, mainly by fire. This is an interesting summary, but the statement of the occurrence of the ling in western Europe, e.g. the British Isles, is hardly accurate. Though it is certainly most characteristic of open heaths it is quite normally associated with *Pinus silvestris*, both native (in Scotland) and subsontaneous (in the south of England) though it does not bear the shade of a dense pine canopy. And it is hardly true to say that *Sphagnum* spp. are its most characteristic associates in oceanic Europe. The ecological range of *Calluna* overlaps that of certain species of *Sphagnum*, but it never attains its greatest luxuriance and is seldom dominant in any sense where *Sphagnum* flourishes. There are several other far more characteristic associates of *Calluna* in the British Isles. It is probable that, as the damper oceanic and suboceanic climates give way to the drier continental, both the closer association with *Sphagnum* and the alternative protection afforded by woods compensate for the lack of climatically moist air. "Xerophily" (Trockenheitsliebe) is an unsatisfactory characterisation of *Calluna*, whose autecology is still by no means fully understood. In one sense, as Stocker showed, it is a hygrophyte. It is physiological ecology, a thorough investigation of the plant's actual water relations in its various habitats, and not only synthetic phytosociology, that is wanted to solve this problem satisfactorily.

A. G. T.

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